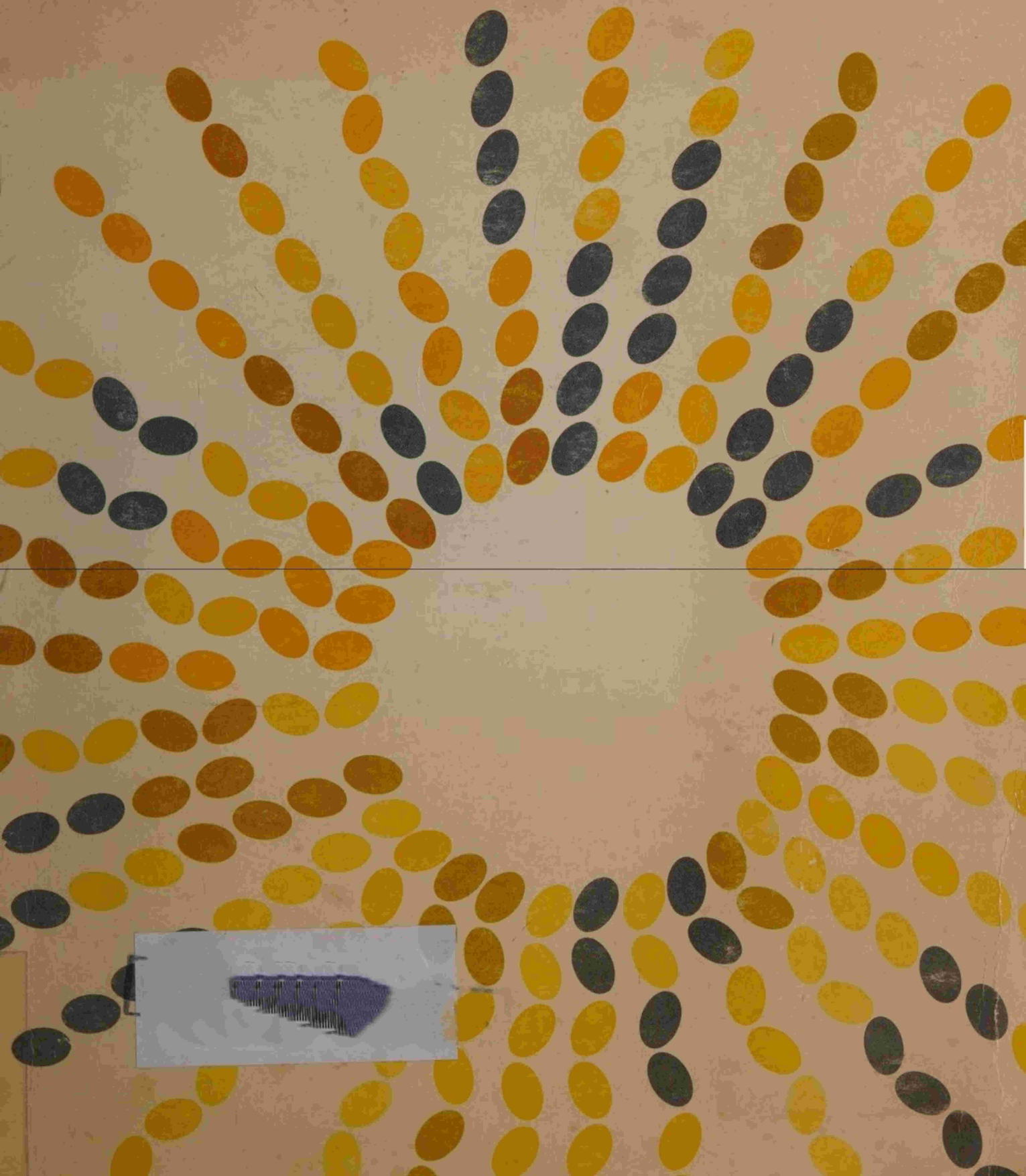




Evolution by natural selection

Species and population





The Open University

Science Foundation Course Unit 20

SPECIES AND POPULATIONS

Prepared by the Science Foundation Course Team

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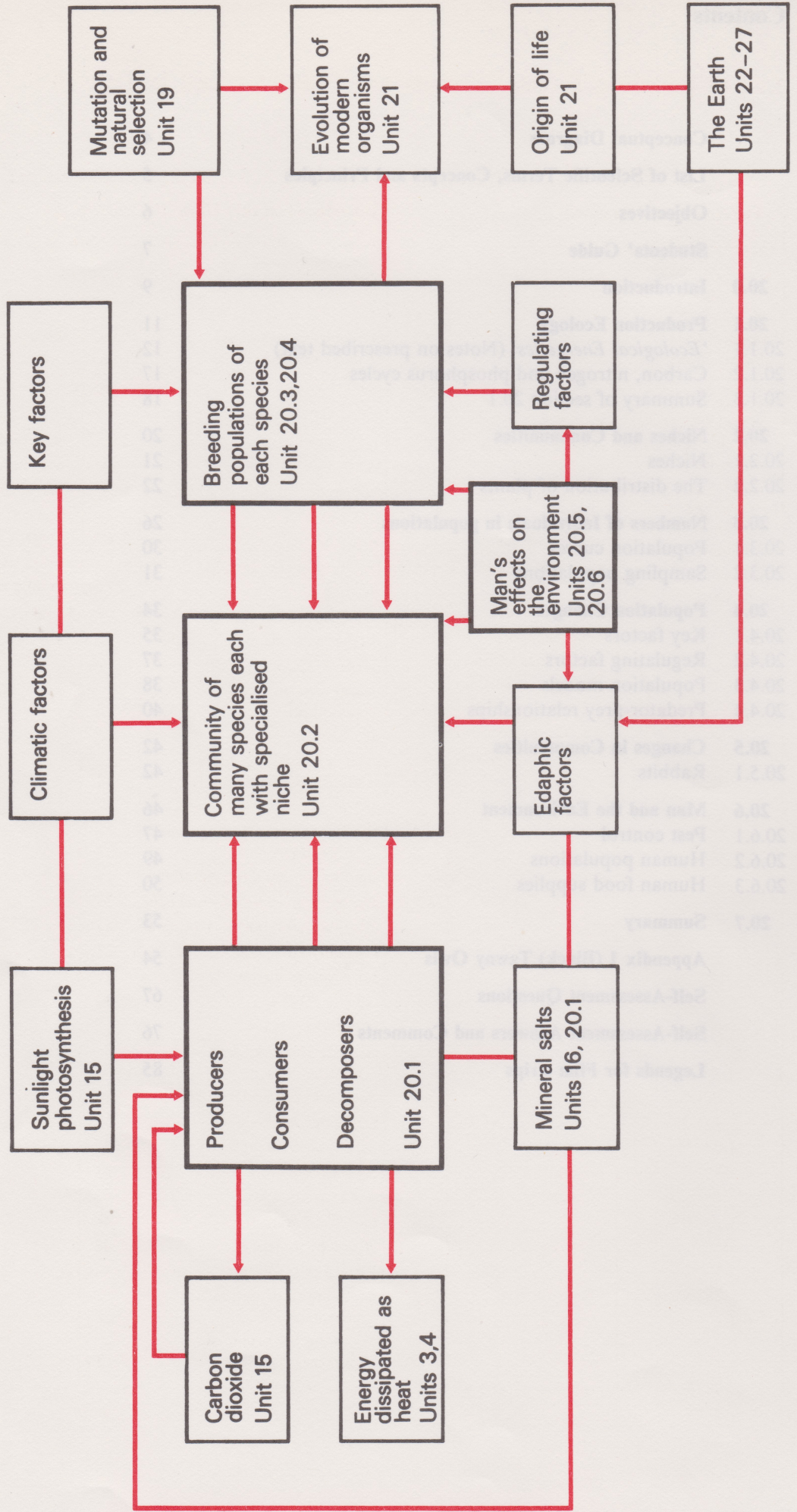


Table A

List of Scientific Terms, Concepts and Principles used in Unit 20

Taken as pre-requisites			Introduced in this Unit			
1	2		3		4	
Assumed from general knowledge	Introduced in a previous Unit	Unit No.	Developed in this Unit or in its set books	Page No.	Developed in a later Unit	Unit No.
general appearance of common types of British vegetation general habits of common British animals main climatic areas of the world	species	19	community (as defined by ecologists)	9	adaptive radiation and specialized niches	21
	natural selection	19	carnivore	11	geochemical cycles	25
	vital activities	18	consumer (= heterotrophe)	11	hydrological cycles	25
	cellular metabolism and energy flow	15, 16	detritus feeder	11	special features of vertebrates, insects and molluscs	21
	photosynthesis	16	herbivore	11	mammals of Australia	21
	protein synthesis	15, 16, 17	producer (= autotrophe)	11	climatic zones of the world	24
			production	13	nitrogen cycle	34
	autotrophes	15	ecological pyramids	14	pollution of the environment	34
	heterotrophes	15	food chains and webs	14		
	aerobic respiration	15	parasite, specific parasite	14		
	calorific value of food	15	energy flow through community	15		
	sexual reproduction	19	decomposer	17		
	exponential increase	2, MAFS	cycling of carbon, nitrogen, sulphur and phosphorus	18		
			niches	21		
			climatic factors affecting plants and animals	22		
			edaphic factors affecting plants	24		
			competition between organisms	25		
			mortality and mortality factors	26		
			fecundity and birth rate	27		
			survivorship curves	28		
			logistic curve	30		
			population cycles	31		
			stability and change in communities	34-36		
			territorial behaviour of birds	34		
			key factor analysis	35		
			density dependent factors	37		
			regulating factors	37		
			weeds and pests	46		
			biological control	48		
			effects of pesticides	48		
			human population explosion	49		
			exploitation of natural resources	51, TV		
			searching behaviour of parasites	39, TV		

Objectives

When you have completed the work for this Unit you should be able to:

1 Define correctly, or recognize the best definitions of, or distinguish between true and false statements concerning each of the terms and principles listed in Table A.

(Tested in SAQs 1, 5, 8, 12, 15)

2 Given relevant information about groups of organisms in a community, either recognize the position of each in given diagrams or construct from this information:

- (a) a food chain or web;
- (b) an ecological pyramid.

(Tested in SAQ 3 and Appendix 1)

3 Given relevant information about organisms to state the part they probably play in:

- (a) the carbon cycle;
- (b) the nitrogen cycle;
- (c) the sulphur or phosphorus cycles.

(Tested in SAQ 4)

4 Given figures in joules for two of the three following processes:

- (a) production;
- (b) respiration;
- (c) consumption of food;

to construct an energy flow diagram for the organisms concerned.

(Tested in SAQs 2, 3)

5 Given relevant information concerning:

- (a) a list of organisms;
- (b) types of environment;

to match organisms and environments.

(Tested in SAQs 6, 18)

6 Draw a population/time graph to show the effect of given changes in environmental conditions on the numbers of individuals in a population or interpret such graphs.

(Tested in SAQ 13 and Appendix 1)

7 Given graphs showing the relation between a given factor and numbers in a population, to recognize whether the factor is:

- (a) a key factor;
- or (b) a regulating factor.

(Tested in SAQ 13 and Appendix 1)

8 Given appropriate information, to calculate and construct mortality or survivorship curves.

(Tested in SAQs 9, 10, 11 and Appendix 1)

9 Choose the most plausible prediction from a given list, given information about changes within a simple food chain, or within a prey-parasite-hyperparasite chain or in a natural community. Suggest experiments to test this prediction.

(Tested in SAQs 17, 18, 19 and Appendix 1)

10 Select from a given list the factors which ought to be investigated before:

- (a) a given foreign species;
- (b) a given chemical substance,

is introduced on a large scale into an environment.

(Tested in SAQ 14)

11 Solve problems related to the geographical distribution of organisms using material drawn from this Unit and Unit 19.

(Tested in SAQs 6, 7)

12 Select from a matrix or recognize as true or false, statements about the following different types of behaviour:

- (a) territorial;
- (b) mating and courtship (from Unit 19);
- (c) searching (for food or host);
- (d) cryptic (concealment) (from Unit 19).

(Tested in SAQ 16)

13 Use the principles given in this Unit to make hypotheses or design experiments or draw conclusions from listed data not treated in the Unit.

(Tested in SAQs 17, 18 and 19 and Appendix 1)

Students' Guide

No organism lives in complete isolation from other organisms. This Unit covers the study of organisms in their environments (the science of 'ecology') and illustrates some of the basic principles involved. We need to discuss species of plants and animals; some of these have precise English names but others have no common names or share names with other species. For the latter, we have given and used the 'Latin name', the internationally recognized name for the genus and species within the Linnean system of nomenclature described in Unit 19. Do not try to learn these names and do not worry if you do not know all the sorts of animals and plants that are mentioned in this Unit. If we did not use named examples the text would be vague and unsatisfactory, but the examples are chosen to illustrate general principles or methods of analysis and it is these principles and methods that are important. Try not to lose sight of the wood for the trees!

There are two prescribed texts for this Unit. You will need to have both these texts beside you while you read, since there are references to figures, tables and text in both books.

There is an order and a pattern underlying the distribution and numbers of plants and animals. In 20.1, we show how communities of organisms are linked together by their energy requirements and need for certain chemical compounds. Part of this section is a commentary on one of the prescribed texts for the Unit. Through the study of 'production ecology', we gain an insight into the relative numbers of different sorts of organisms and some of the factors that limit the size and complexity of communities.

In 20.2, the structure of communities is approached from a different point of view, that of the parts played by the many species that compose them. Each species occupies a 'niche' (defined in 20.2); comparable niches may be occupied in different parts of the world by different species. We study some of the factors controlling the distribution of species through the world.

Quantitative studies of populations depend on collecting and counting samples and then analysing the numbers obtained. In 20.3, we consider how population numbers change as organisms grow older and how populations are affected by birth rates and death rates.

Studies of numbers of individuals in populations show that some species are rare and others are common but for both types of species there are fluctuations; some of these are regular 'cycles', but others are irregular and, at present, unpredictable.

'Population dynamics' is the study of population numbers and how and why they vary; this is the subject of 20.4. If sufficient relevant information is available, then it is possible to identify the causes of death that are responsible for the fluctuations and also to identify other causes of death that vary in such a way that the population numbers tend to return towards the average values. If you are having difficulty, then you should read rapidly through this section without attempting to work out the figures for yourself.

Appendix 1 (Black) is a structured exercise to give you practice in applying methods and principles mentioned in sections 20.1, 20.3 and 20.4.

Communities are generally close to a state of balance under natural conditions but change slowly with time. Interference with a community is likely to lead to rapid changes—in our present state of knowledge, some of these changes may be unexpected and drastic. Some of the effects of the sudden reduction in numbers of rabbits after the onset of myxomatosis in Britain are discussed in 20.5.1.

The impact of man on the environment is currently receiving much publicity. In 20.6 we consider some of the biological implications of modern agricultural methods, particularly in relation to weeds and pests. The human population explosion is creating serious problems, discussed in 20.6 from the point of view of production ecology. Human survival may depend on rational exploitation of food resources, some of which are at present over-exploited, as illustrated in the TV programme.

The study of ecology, of the principles underlying the complex patterns of species distribution and community structure through the world, is of fundamental importance for human survival. Here in Unit 20 you meet some of the modern ideas and methods of this fast-growing branch of biology.

20.0 Introduction

In Unit 19 you learnt what biologists mean by the term 'species' and that they believe that modern species have evolved by modification from pre-existing species. The most probable mechanism for this evolution is natural selection which acts on a group of individuals that form an interbreeding population. The genes of these individuals form part of a 'gene pool' on which selection acts so that at any time the 'wild' population will be well adapted to the environment in which it lives. Since individuals that are less well adapted are less likely to survive than the others, the 'survival of the fittest' means competition among individuals of the same species—a form of intra-specific competition.

In this Unit we are more concerned with inter-specific relationships, with the interactions between the many species of organisms living in the world today. The study of organisms in their environments—environmental biology—is called *ecology* (from the Greek for 'house'). At present there is considerable public interest in and awareness of the effects of man's activities on the environment and so on other species of organisms. Some special examples of this are included in Units 10 and 34. In this Unit we shall study the basic principles of ecology—the principles which govern the distribution and sizes of populations of organisms throughout the world.

As with most sciences, the early development of ecology was as a descriptive science, based on the compilation of lists of organisms present or absent from various places. Naturally, it is still important to know the distribution of different organisms and to understand the factors controlling this; these are discussed in 20.2. When species are listed for different areas, it is apparent that they form non-random associations which are called *communities*. These are formed of populations of different species found together in a definite area. Each community exists in a non-living environment made up of the medium (earth or water, or both) and the local climate. The community studied with its environment makes up an *ecosystem*. Communities and ecosystems can be studied at different levels—for instance, the community of an oak-wood includes a large number of smaller communities such as those of the oak-trees, the hazel shrubs, the herbs under the trees, the litter of fallen leaves and so on.

The oak-wood itself is part of a terrestrial ecosystem, probably a lowland area of Britain, which in turn is part of the island ecosystem of Great Britain. Even this island ecosystem is not a unit independent of all others, since birds and butterflies and other less conspicuous organisms, as well as people, can move in and out from neighbouring continental areas. Thus it is necessary to define communities carefully when discussing and comparing them.

Ecologists have moved from the purely descriptive approach to two main lines of quantitative research. The first is the study of the structure of communities in terms of the throughput of energy and chemical compounds. This is called *production ecology* and we shall discuss its principles in section 20.1. The second quantitative approach is the study of the numbers of organisms of different species and how they vary in time and space and why they are common or rare. This is called *population dynamics* and it forms the content of sections 20.3 and 20.4.

ecology

communities

ecosystem

Of course, all these types of approach are necessary for a complete understanding of the distribution of species of organisms in the world and of the size of their populations—an ideal far from achieved at present. The better scientists understand ecological principles, the better able they will be to predict the results of interference with existing communities by man or by any other agency. In sections 20.5 and 20.6 we shall discuss some examples of such interference.

Reading

There are two prescribed texts:

John Phillipson, *Ecological Energetics*. Arnold, 1966.

Maurice E. Solomon, *Population Dynamics*. Arnold, 1969.

You will be directed to read certain sections and to look at certain figures and tables in both books. If you wish, you may read the whole of both books, treating them as black-page appendices.

If you wish to read one of the recommended books, you will find the following chapters are relevant to this Unit:

N. J. Berrill, *Biology in Action*. Heinemann, 1967. (Chapters 32 and 33.)

S. D. Gerking, *Biological Systems*. Saunders, 1969. (Chapters 5, 9 and 22.)

P. B. Weisz, *The Science of Biology*. McGraw-Hill, 1967. (Chapters 8, 9, 10 and 17.)

Rachel Carson, *Silent Spring*. Penguin, 1965. (This book was written in 1962 and started the concern for the environment that has increasingly made an impact in Europe and USA.)

K. Mellanby, *Pesticides and Pollution*. Fontana, 1969.

20.1 Production Ecology

Although production ecology is a more recent development than descriptive ecology, it provides a logical basis for the structure of communities, so it is sensible to study it first. A real understanding of the processes which determine the level of production is also essential for rational exploitation of world resources of food for the increasing human population—we shall refer to this again in 20.6.

The vital activities of all organisms (refer to Unit 18, section 2.1, if you need to remind yourself about them) depend on 'the use of energy'. As you read this text, you are moving your eyes, you are breathing, your heart is beating, your guts are digesting and assimilating food and nerve cells in your brain are active. As you read in Units 15 and 16, all this activity depends on biochemical processes in your body cells. These processes stop in dead organisms. One way of dying is through starvation, i.e. lack of raw materials essential for the biochemical processes. Thus life depends on the supply and utilization of certain raw materials and we can think of these as the source of energy for life processes (vital activities).

Photosynthesis is characteristic of plants. Summarize the main features of this method of feeding by answering the following questions:

- 1 What are the raw materials needed by the plant?
- 2 What does the plant synthesize?
- 3 Where does the energy for photosynthesis come from?

The plant grows by producing more plant cells; proteins are essential components of cells.

autotrophes

- 1 Carbon dioxide and water.
- 2 Carbohydrates—sugars which may then be converted into storage products such as starch.
- 3 Sunlight—energy is made available in the chloroplasts in the plant cells (usually in leaves of land plants).

Beyond those already mentioned, what substances do plants require for the synthesis of proteins?

Compounds containing nitrogen, phosphorus and sulphur. Plants use inorganic salts—nitrates, phosphates and sulphates—and these are often collectively called 'mineral salts'.

Since plants can synthesize their proteins entirely from inorganic substances—water, carbon dioxide, mineral salts—if provided with the appropriate wavelengths of light, they are called *autotrophes* (from the Greek for 'self' and 'food'). Organisms which cannot synthesize proteins from inorganic substances, but must obtain their amino acids by digestion of proteins manufactured by some other organism, are called *heterotrophes* (from the Greek for 'different' and 'food'). Typically these organisms cannot synthesize sugars either, and must obtain these from some other organism. Animals are heterotrophes; so are some plants such as the fungi (mushroom, moulds). So the growth of animals depends on them eating other organisms, living or dead. If they eat plants, as cows do, the animals are called *herbivores* (from the Latin for 'grass' and 'devour'); if, like lions, they eat other animals, they are called *carnivores* (from the Latin for 'flesh' and 'devour'). Animals, such as earthworms, that feed on fragments of decaying plant and animal material are called *detritus feeders* (from the Latin for 'wearing away').

herbivores
carnivores

detritus feeders

The release of energy within cells and the uses made of this energy were discussed in Units 15 and 16. There are some organisms, such as yeasts and various bacteria, that have unusual metabolic pathways, but most cells and organisms depend on aerobic respiration. Ultimately, they depend on absorbing oxygen from the environment; the uptake of this can be measured, often very accurately. Glucose is the substrate that is usually metabolized during tissue respiration; fats and proteins are metabolized in some organisms and under certain conditions, but these are much less common substrates than glucose. Thus it is generally reasonable to deduce the total output of energy of an organism or group of organisms by measuring the amount of oxygen absorbed from the environment and calculating how many joules* would be available were this oxygen all used in the tissue respiration of glucose. From respiration of 180 g of glucose, 283×10^4 J would be made available for the organism's activities.

respiration and energy

Heterotrophes (animals) obtain all their energy from their food. Often it is possible to measure the amount of food that is eaten; the energy thus taken into the animal can be calculated from the calorific value of the food (refer to Unit 15 for more information about this). If the food intake and oxygen uptake are known, an energy balance can be set up:

$$\begin{array}{lcl} \text{Calorific value of food} & = & \text{output of energy calculated from} + X \text{ joules} \\ \text{(in joules)} & & \text{the amount of oxygen absorbed} \\ & & \text{(in joules)} \end{array}$$

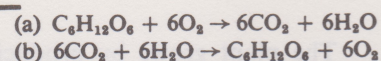
food and energy

If X is a positive value, then the organism is able to grow or to lay down food reserves (e.g. fat deposits) or to produce reproductive bodies (e.g. eggs and sperm). But if X is negative, the organism may be using up food reserves or wasting away.

With autotrophes (green plants), the measurement of oxygen absorbed in respiration is complicated because the plants perform photosynthesis.

Show this by writing two equations:

- to summarize the process of respiration, in which glucose is converted to CO_2 and water;
- to summarize photosynthesis, generating glucose from CO_2 and water.



Suggest how (a) respiration and (b) photosynthesis could be measured for plants.

In practice, similar plants or collections of plants are set up in closed vessels, one exposed to light and the other in a black, light-proof container. The change in amount of oxygen in the two containers is measured:

Plants can only perform photosynthesis in light but they must respire both in light and in the dark. So it is possible to measure respiration as the uptake of oxygen by a plant in the dark. To measure photosynthesis, the plant must be in light. It will produce more oxygen than it uses in respiration but a correction must be made, adding the volume of oxygen consumed in respiration.

How is the total amount of oxygen produced by photosynthesis obtained?

By adding the amount of oxygen used up in the dark to the amount of oxygen produced in the light (after suitable adjustments for amount of material in the two containers). The plants in the light respire as well as perform photosynthesis; it is assumed that they respire at the same rate as similar plants in the dark.

20.1.1 Ecological energetics

This section is concerned with energy 'budgets'. The relationship between organisms and their environment in terms of the acquisition and dissipation of energy is important to ecologists interested in natural communities;

* You will find that many books and articles including your prescribed text use calories or kilocalories (kcal) as units for energy instead of joules (the SI unit). To convert calories or kilocalories into joules, multiply by 4.2 or 4.2×10^3 respectively. The actual conversion factor is 4.184 or 4.184×10^3 but 4.2 is sufficiently accurate for most purposes.

it is also very important for the rational exploitation of world food resources, as we shall show in 20.6.

While studying this section, you will be referred to your prescribed text, *Ecological Energetics*. You will be told to read the following sections of that book: 1.6, 2.2, 2.4, 3.2 and 3.3 (adding up to about 4 000 words). Before you start to read each section, you should read the commentary on it in this text. Definitions of unfamiliar names and terms are given here. Note that the unit for energy in the book is the calorie or the kilocalorie (equivalent to 4.2 or to 4.2×10^3 joules).

DO NOT ATTEMPT TO MEMORIZE THE FIGURES OR NAMES.

Section 1.6 *Energy transformations in nature*

Start reading on page 5, section 1.6, 'Energy transformations in nature'. Note the term 'production'—this is only loosely equivalent to the word 'productivity' as used in ordinary speech. Production is a measure of the total amount of new living matter formed per unit time; even if some part of this matter dies (or is consumed by some other organisms) during the time interval, it must still be included in the gross production. Since net production is gross production minus energy released in respiration, the matter which has died or been consumed by some other organism is also included in 'net production' for that time. You will meet examples of this later.

production

Definitions

incident energy—the energy of the sunlight falling upon a particular place, including that of all wavelengths, visible and invisible (see Unit 2).

efficiency—is usually measured by expressing the amount of energy utilized by the particular organism being studied as a percentage of the total energy available to it. Efficiency is never 100 per cent!

chemical energy—calorific value.

sensible heat—heat that can be felt by man.

perennial grass-herb vegetation of an old-field community—the grasses and small flowering plants in a field which has gone out of cultivation.

exudate—secretion produced by plants, such as nectar and sap flows.

peat deposition—plant matter decays very slowly under certain conditions and the decaying plants accumulate to give a brown or black soil called peat (dried, this is highly combustible and still used widely as fuel in parts of Ireland).

faeces—these are the remains of food taken into the body but not assimilated.

excretory products—these are waste substances produced within the body and then discharged, e.g. urine and sweat. The term 'excreta' in ordinary speech usually includes faeces but, scientifically, faeces and excreta are different in origin since the former have never been assimilated into the body whereas the latter are by-products of metabolism.

Now read section 1.6; then return to this text.

Section 2.2 *Food webs*

When a plant is eaten by one animal which in its turn, is eaten by another, the sequence of events can be expressed thus:

Plant → Herbivore → Carnivore.

This is called a *food chain*. You should be able to think of many possible food chains—here are three examples:

Lettuce → Snail → Thrush;

Grass → Vole (small rodent related to mouse) → tawny owl;

Grass → Sheep → Man.

Phillipson gives other examples (using the scientific names) in section 2.1. He then points out, in section 2.2, that the food chains in natural communities branch and overlap with each other to give complex patterns, called *food webs*. As an example, he considers the feeding relationships of the herring and illustrates this in Figure 2.1. All the organisms mentioned in the text are shown in the figure. Note that the arrows show the direction of feeding, *not* the direction of energy flow (as is the convention in the food chains above and the one on page 10 of the book). The herring eats sand eels, so energy from sand eels flows to the herring. In Figure 2.1, the organisms at the bottom of the diagram (diatoms and flagellates) are small floating plants. If you read Appendix 1 of Unit 18, you will have met them already. The organisms that feed on this *phytoplankton* (this is the term for small plants that live in the upper layers of the sea and lakes and drift with water currents) are called *zooplankton*. This means small animals that live in the upper layers of the sea and lakes; some of them are sometimes called 'water fleas'. The layer above the zooplankton in the diagram includes one fish, the sand eel, and three other unfamiliar organisms that are small but predatory.

food chains and webs

Now read section 2.2; then return to this text.

Section 2.4 Ecological pyramids

The idea of constructing ecological pyramids proved a very helpful step forward in quantifying ecological observations, so it is important that you should understand about the different sorts of pyramid. Each type has its uses and its limitations; these are pointed out in this section of the book.

pyramids of numbers

Figure 2.2 Do not try to identify the organisms, but simply look at this as an example of a complicated pattern—in this case, based on the community of a small stony stream.

Figure 2.3 *Parasites* are organisms which obtain all their food from another organism, the host, which is usually much larger than its parasite. Usually the parasite lives on or in its host for most of its life. *Hyperparasites* are parasites of parasites—and therefore smaller than their hosts, the parasites of a larger host. Plant parasites include aphids (greenfly and blackfly) and other 'plant-bugs'; these insects may have roundworms as parasites inside them; they probably also have bacterial parasites.

Figure 2.4 Phytoplankton and zooplankton have already been defined when discussing the food of the herring.

The dry weight is obtained by heating the organisms in an oven at about 80° C until there is no further change in weight. All the water should then have evaporated and all other components of the body should remain and be weighed. The bodies of most organisms are about 60 per cent water; some organisms, such as jellyfish, have more than 99 per cent of water in their wet weight.

Text below this figure Algae are simple plants. The group includes phytoplankton, such as the diatoms; these are the microscopic forms referred to here.

Figure 2.5 P=producers; H=herbivores; C=carnivores; T.C.=top carnivores. Look at the shape of the pyramid; ignore the words and figures. The data used for this diagram are shown in a different form in Figure 3-2 (see later).

Text below this figure *Ensis* is a razor shell, quite common on some sandy beaches where it burrows near the low tide level. *Calanus* is shown in Figure 2.1; it is a water flea that is a very important part of the diet of the herring.

Now read section 2.4; then return to this text.

Section 3.2 Energy flow models

The pyramid in Figure 2.5 shows the amount of energy utilized in one year by the organisms on or over one square metre of a spring-fed river in Florida. The rate of energy utilization of the different trophic levels (producers, herbivores, carnivores, etc.) can be expressed in other ways; one is shown in Figure 3.2. This is called an energy flow diagram because it indicates the sources from which each trophic level draws its energy and the actual fate of that energy; thus the complete diagram follows the fate of all the energy entering that area and available to organisms.

energy flow diagrams

Look at Figure 3.2 (page 28).

At the left is the amount of energy entering the system—the energy in the light absorbed by the plants in the spring. As a result of photosynthesis, about 21×10^3 kcal/m²/yr of plant material is produced (from 410×10^3 kcal of energy absorbed by the plants). The plants respire, using about 12×10^3 kcal, so that about 9×10^3 kcal of plant material is available as potential food (and source of energy) for herbivores. But some of this plant production leaves the area (as algae or bits of flowering plants washed downstream) and some dies and so is only available to organisms called *decomposers*. So the actual amount of energy as plant material available to herbivores is 3.37×10^3 (with 5.95×10^3 going to decomposers or to export and 0.49×10^3 entering the spring as imported plant material).

Following the diagram to the right, you can see that the potential food energy available to first level carnivores is only 383 kcal (out of the 3.37×10^3 kcal available to herbivores).

How much energy is dissipated as heat, as a result of respiration of the herbivores?

1 890 kcal—this is shown in the stippled area leading from the rectangle labelled 'Herbivores' to the block labelled 'Total heat.'

The production of first level carnivores is only a fraction of the production of herbivores (383 kcal compared with 3 368 kcal). The first level carnivores respire and are also available for export and for decomposers and as food for production of top carnivores. Look at the diagram and answer the following questions.

What proportion of the energy available as food to first level carnivores is dissipated as heat through respiration? What proportion goes into the production of top carnivores?

316/383 kcal is dissipated as heat during respiration and 21/383 kcal goes into production of top carnivores, representing about 83 per cent and about 5.5 per cent respectively of the food energy.

Look now at the block labelled 'Decomposers'. Compare the energy of the material available as food to the decomposers with the dissipation of heat as a result of their respiration. The food energy for decomposers is 5.06×10^3 kcal and the heat dissipated is 4.6×10^3 kcal (about 91 per cent of the food energy). Notice that the decomposers provide food for more decomposers, but this is only about 9 per cent of the total food of decomposers (0.46×10^3 compared with 5.06×10^3 kcal).

Finally, compare the total heat dissipated as a result of respiration of plants (12×10^3 kcal), herbivores and carnivores ($1.9 + 0.3 + 0.13 = 2.33 \times 10^3$ kcal) and decomposers (4.6×10^3 kcal) with the gross production of plants. The total heat dissipated through respiration of the whole community is 18.93×10^3 kcal and the gross production of plants is 20.8×10^3 kcal—the difference is explained by the figures for export and import of material. But remember that the gross production of plants represents only a fraction of the energy in the light absorbed ($21/410 \times 10^3$ kcal or just over 5 per cent). The other 95 per cent of the incident light energy is not utilized by the plants and so is not available to any of the animals.

respiration and production

Now look at Figure 3.1 (page 25).

This is an energy flow diagram for another freshwater spring in USA. Ignore the figures inside the boxes (which indicate changes in standing crops). The other figures, mostly associated with arrows, are comparable with those in Figure 3.2. The stippled areas represent energy dissipated as respiration. There is a misprint—the respiration of micro-organisms should be 295 kcal, not 2.95; Notice that there is no figure for the input of energy as light. Plants are represented as a small box labelled 'algae' from which 655 kcal are available as potential food for herbivores. The total energy available for production of herbivores is given as 2 300 kcal:

Where does most of this come from?

It comes from 'Debris' 2 350 kcal less 705 kcal flowing to 'Deposit' and 'Micro-organisms'.

If you find this confusing, you are justified in doing so! The category 'Herbivore' in this diagram actually consists largely of organisms that are called 'decomposers' in Figure 3.2. These are animals that eat debris of plant origin; some also eat living plants such as algae attached to stones or to sticks, so that it is difficult to separate 'pure' herbivores from animals with wider feeding habits.

The term *herbivore* is used for the primary consumers in Figures 3.1 and 3.2. That these feed on plant debris in one, and on live plants in another, is a real difference between the two communities; this difference is discussed in the first paragraph of section 3.2. *Detritus* is the term for dead organisms in various states of breakdown; it usually consists largely of sticks and leaves.

grazing and detritus food chains

When you look at Figure 3.3, to compare the grazing food chain with the detritus food chain (these are explained in the first paragraph), the figures you should compare are the following. For the marine bay, the food energy available from the phytoplankton (the producers) is 8 kcal; of this, 6 kcal pass (as living algae) along the grazing food chain and 2 kcal (as dead algae) along the detritus food chain. For the forest, the food energy available as leaves (from the producers, the trees) is 12 kcal; of this, 2 kcal pass (as green leaves on the tree) along the grazing food chain, while 10 kcal pass (as dead leaves forming 'litter' on the ground) along the detritus food chain.

Do not worry about the other details of these two diagrams.

Now read section 3.2; then turn back to this text.

Section 3.3 *Decomposers*

Comparison of the four energy flow diagrams referred to in section 3.2 has revealed the importance of dead organisms as a source of food energy. You may have wondered what sorts of organisms consume detritus and corpses. These decomposers are discussed in section 3.3, where experimental evidence is presented to show the importance of larger detritus feeders in enabling bacteria and other micro-organisms to attack dead leaves. Do not worry if you do not know all the organisms mentioned in the text—the point is to realize the complementary effects of the larger and smaller organisms and that both are important in the energy budgets of communities.

Now read section 3.3; then return to this text.

We shall refer to some figures and tables in *Ecological Energetics* later in the text. You may read the whole book, if you wish, treating the rest of it as equivalent to a black-page Appendix.

decomposers

Key:

- Food chain
- Death
- Conversion of dead proteins
- Metabolism of large organisms
- Synthesis of protein and carbohydrates
- Man's activities
- Metabolism of micro-organisms

20.1.2 Carbon, nitrogen and phosphorus cycles

In production ecology, as you have read in *Ecological Energetics*, 'energy' is traced from the sun, through plants, herbivores and carnivores of the grazing food chain and their dead bodies, and then through the detritus food chain. At each link of the chain, energy is 'dissipated' as a result of respiration and ceases to be available for the activities of organisms. Only part of the energy represented by plant production is 'fixed' by animals as production of herbivores; only part of herbivore production is transformed into carnivore production and so on. Without plants performing photosynthesis, production at all other trophic levels would eventually stop, as illustrated in Figure 1. 'All flesh is grass' is a true statement if it is read as 'all other living organisms are ultimately dependent for survival on autotrophes and especially on photosynthetic autotrophes'!

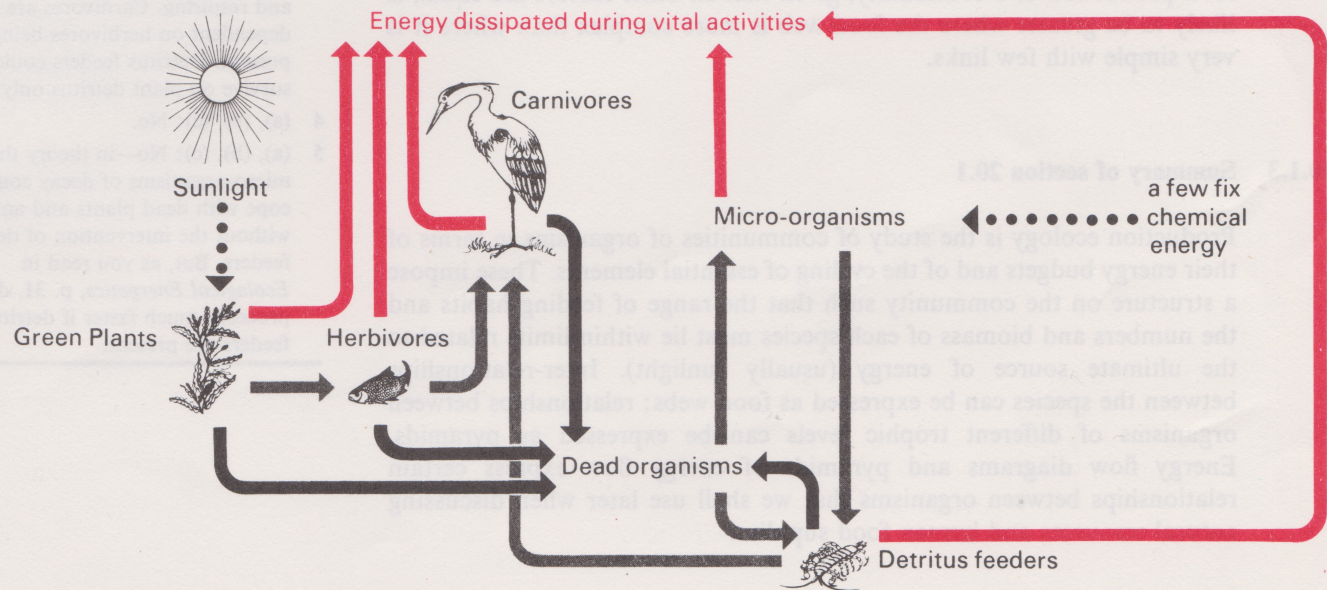


Figure 1 Diagram to illustrate the 'flow' of energy through a community of organisms.

Food webs are concerned with more than the 'flow' of energy from plant to herbivore to carnivore and so on. Plants synthesize proteins from simple raw materials—in the case of green plants, from water, carbon dioxide and mineral salts; herbivores obtain all their amino acids from the proteins of producers; carnivores obtain theirs from the proteins of herbivores.

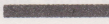
Do you expect the elements carbon, hydrogen, oxygen, nitrogen, phosphorus and sulphur (the constituents of proteins) to be dissipated and 'lost' to living organisms as energy is?

Or would you expect these elements to be 'cycled' and utilized again by living organisms?

In fact, they are 'cycled'. Figures 2, 3 and 4 show the fates of carbon, nitrogen and phosphorus. Sulphur cycles in much the same way as phosphorus. Hydrogen and oxygen cycles are more complex, so we will not describe them here.

Micro-organisms convert proteins of dead organisms through various intermediates into carbon dioxide, water and inorganic salts (usually referred to as 'mineral salts').

Key:

-  Food chain
-  Death
-  Conversion of dead proteins
-  Metabolism of large organisms
-  Synthesis of protein and carbohydrates
-  Man's activities
-  Metabolism of micro-organisms

micro-organisms

Examine the Figures 2, 3 and 4, then answer the following questions:

Are the following types of organisms essential for the complete cycling of (a) carbon, (b) nitrogen, (c) phosphorus?

- | | |
|--------------------|-------------------|
| 1 green plants | 2 micro-organisms |
| 3 herbivores | 4 carnivores |
| 5 detritus feeders | |

The presence in most communities of herbivores, carnivores and detritus feeders in addition to plants and micro-organisms results in a faster turnover of the essential elements carbon, nitrogen, sulphur and phosphorus. This is because the respiration of the animals yields CO_2 , their excretion yields principally nitrogenous compounds, and their activities produce dead organisms and assist in their physical destruction. So the total production of a community, given that all other factors are equal, is likely to be greater where the food web is more complex than where it is very simple with few links.

20.1.3 Summary of section 20.1

Production ecology is the study of communities of organisms in terms of their energy budgets and of the cycling of essential elements. These impose a structure on the community such that the range of feeding habits and the numbers and biomass of each species must lie within limits related to the ultimate source of energy (usually sunlight). Inter-relationships between the species can be expressed as food webs; relationships between organisms of different trophic levels can be expressed as pyramids. Energy flow diagrams and pyramids of energy flow express certain relationships between organisms that we shall use later when discussing natural resources and human food supplies.

- 1 (a), (b), (c): Yes.
- 2 (a): No. (b), (c): Yes, unless man synthesizes massive amounts of fertilizer at enormous energy cost.
- 3 (a), (b), (c): No—plants in theory could survive without any animals being present, but they would be strictly limited by the amount of CO_2 present, since only plants and micro-organisms would be alive and respiring. Carnivores are strictly dependent on herbivores being present. Detritus feeders could survive on plant detritus only.
- 4 (a), (b), (c): No.
- 5 (a), (b), (c): No—in theory the micro-organisms of decay could cope with dead plants and animals without the intervention of detritus feeders. But, as you read in *Ecological Energetics*, p. 31, decay proceeds much faster if detritus feeders are present.

Now you can do SAQs 1 to 4.

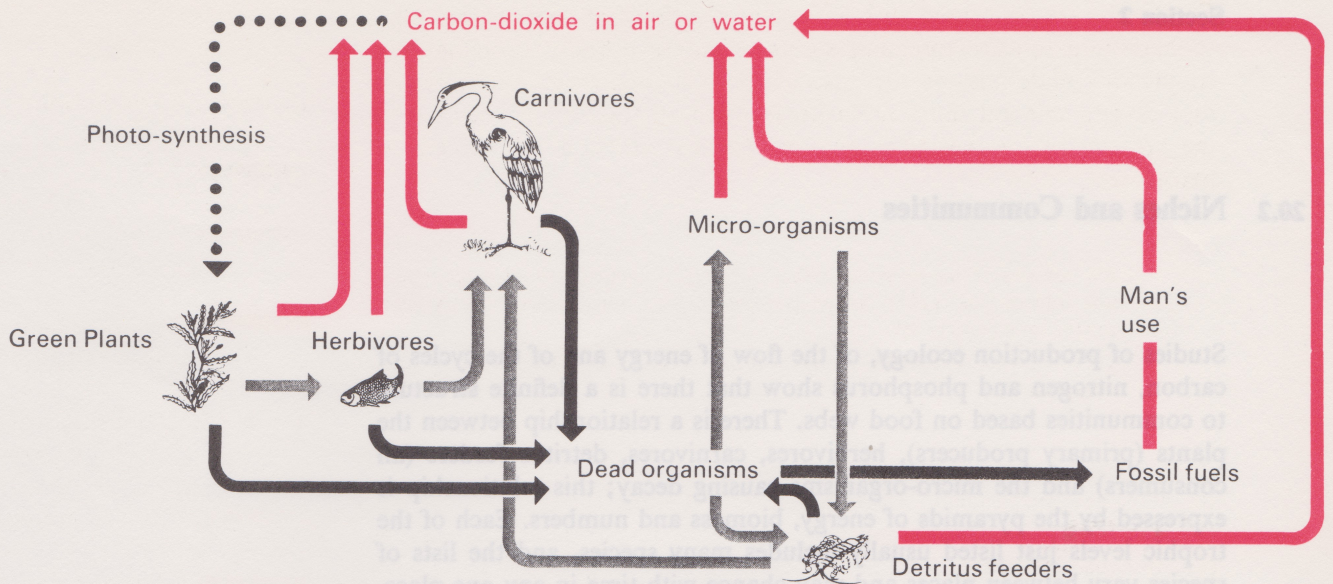


Figure 2 The carbon cycle.

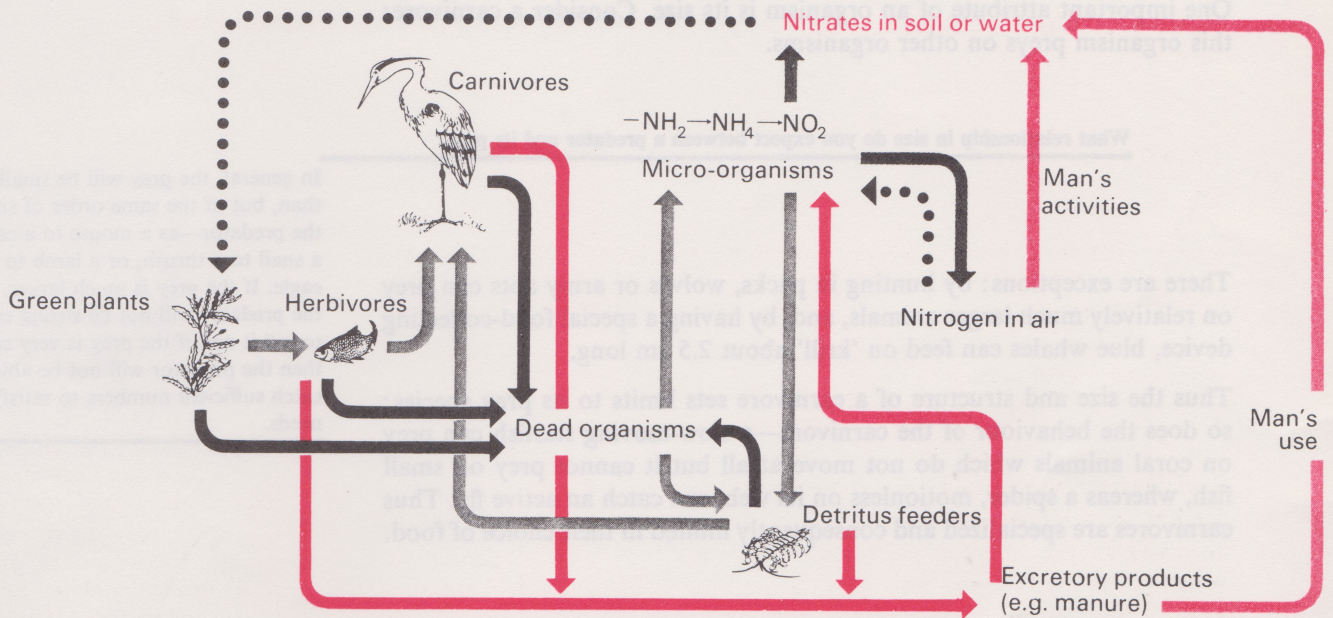


Figure 3 The nitrogen cycle.

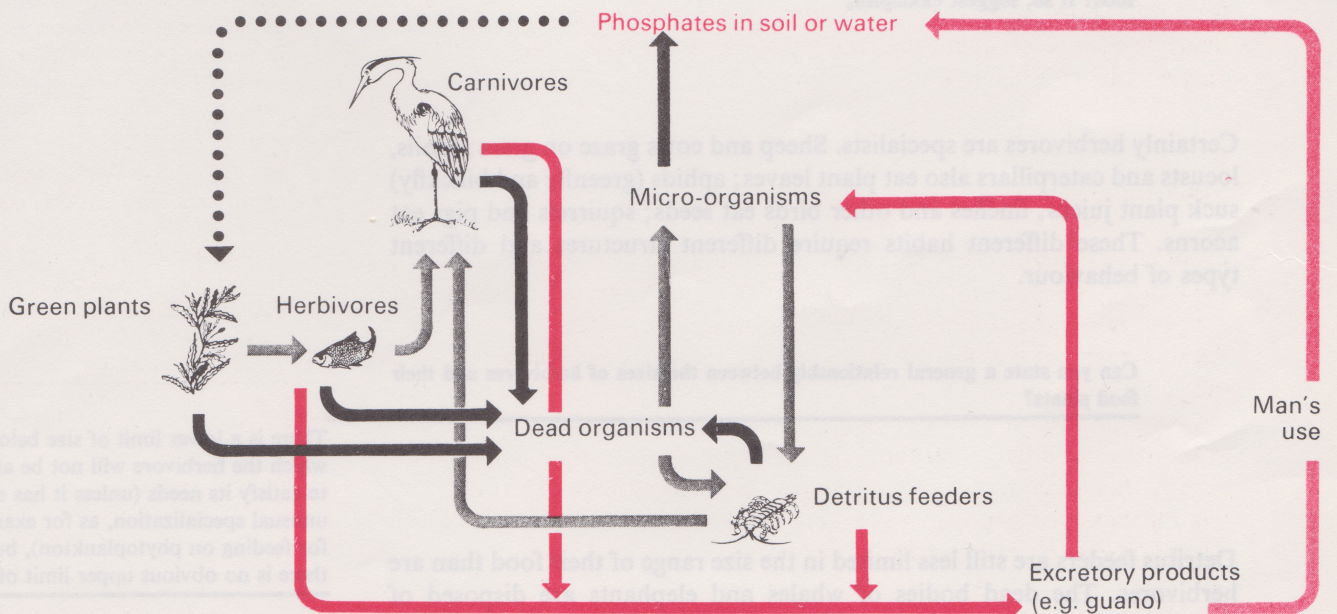


Figure 4 The phosphorus cycle.

20.2 Niches and Communities

Studies of production ecology, of the flow of energy and of the cycles of carbon, nitrogen and phosphorus show that there is a definite structure to communities based on food webs. There is a relationship between the plants (primary producers), herbivores, carnivores, detritus feeders (all consumers) and the micro-organisms causing decay; this relationship is expressed by the pyramids of energy, biomass and numbers. Each of the trophic levels just listed usually includes many species, and the lists of species vary between places and may change with time in any one place. So let us examine the composition of communities in greater detail.

One important attribute of an organism is its size. Consider a carnivore: this organism preys on other organisms.

What relationship in size do you expect between a predator and its prey?

There are exceptions: by hunting in packs, wolves or army ants can prey on relatively much larger animals, and, by having a special food-collecting device, blue whales can feed on 'krill' about 2.5 cm long.

Thus the size and structure of a carnivore sets limits to its prey species; so does the behaviour of the carnivore—a slow-moving starfish can prey on coral animals which do not move at all but it cannot prey on small fish, whereas a spider, motionless on its web, can catch an active fly. Thus carnivores are specialized and consequently limited in their choice of food.

Do you expect herbivores also to be specialists and limited in their choice of food? If so, suggest examples.

Certainly herbivores are specialists. Sheep and cows graze on grass; snails, locusts and caterpillars also eat plant leaves; aphids (greenfly and blackfly) suck plant juices; finches and other birds eat seeds; squirrels and pigs eat acorns. These different habits require different structures and different types of behaviour.

Can you state a general relationship between the sizes of herbivores and their food plants?

Detritus feeders are still less limited in the size range of their food than are herbivores. The dead bodies of whales and elephants are disposed of equally with those of crabs and mice. Parasites, on the other hand, are limited to hosts that are larger than themselves, usually much larger.

In general, the prey will be smaller than, but of the same order of size as, the predator—as a mouse to a cat, or a snail to a thrush, or a lamb to an eagle. If the prey is much larger, then the predator will not be strong enough to kill it and if the prey is very small, then the predator will not be able to catch sufficient numbers to satisfy its needs.

There is a lower limit of size below which the herbivore will not be able to satisfy its needs (unless it has some unusual specialization, as for example for feeding on phytoplankton), but there is no obvious upper limit of size.

Specialized habits and activities of organisms are the basis for the concept of 'niche', proposed by Elton in his classic book *Animal Ecology* in 1927. In a human community such as a town or village, there are recognizable niches such as policeman and publican and shop-keepers of different kinds. Each title conveys the function of the individual and some of his attributes, e.g. the policeman must be over a minimum height, but the others could be tall or short. Similar niches may be present in human communities in different parts of the world, showing interesting similarities and differences—for instance, monarchs, presidents and prime ministers. For animals, the niche can often be defined by its size and food habits, but other habits are also relevant.

When communities of organisms have been broken down into niches, the species filling these in different places can be identified and compared. Take, for instance, the herbivores feeding on oak-trees: these can be classified into large herbivores and small herbivores, both eating leaves; herbivores feeding on sap; herbivores living as parasites in the leaves; herbivores feeding on other plants which grow on the oak such as the alga *Pleurococcus* (which forms a thin powdery green covering over the bark of the tree usually on the north-facing side) and lichens.

List these herbivores if you can from general knowledge by filling the spaces below:

- (a) large leaf-eaters:
- (b) small leaf-eaters:
- (c) small sap-eaters:
- (d) parasites:

niches

- (a) deer
- (b) caterpillars
- (c) aphids
- (d) gall insects

The herbivores on *Pleurococcus* and lichens are woodlice, caterpillars, millipedes and slugs.

From your general knowledge, identify similar niches and the animals filling them on cultivated herbs and grasses (i.e. on fields of crops or market gardens or parks and family gardens).

- large leaf-eaters: cattle, sheep; sometimes deer, rabbits.
- small leaf-eaters: caterpillars, snails, slugs, beetles, grasshoppers.
- parasites: eel-worms, root-fly larvae.
- small sap-feeders: aphids, scale insects.

The smaller plants are probably also present but growing on the ground, not on the cultivated plants—they will have similar herbivores to those in the wood. You will have realized that the second list is very similar to the first list—it is only when the *species* are listed by name that the two lists look very different. For instance, compare these lists of common caterpillars found on various plants:

<i>oak</i>	<i>pine</i>	<i>cabbage</i>	<i>nettles</i>
winter moth	bordered white	cabbage white	small tortoiseshell
green tortrix	pine beauty	diamond back moth	pearl moth

All eat the leaves and have similar jaws; they all have similar life-histories—the full-grown caterpillar forms a pupa (chrysalis) and later emerges as the adult moth or butterfly; the adult lays eggs which hatch into caterpillars. So the feeding niches are identical, but filled by different species on the different plants.

caterpillars and plants

Some of the insects which live on oak-trees will live only on this species, whereas some are able to eat the leaves of several or many species of tree. Each tree species has associated with it some insect species which feed only on it.

The specificity of herbivores is a very important facet of community structure. It explains why some animals are absent from some places—simply because their food plant is absent.

All the examples of niches given so far have been of herbivores, but there are plenty of other types of niche in the other trophic levels, as well as further herbivore niches not listed here. Elton quoted some examples showing remarkable parallels in very different places. One is the ‘tick-picker’—a carnivore that picks parasites off the outside of their hosts. In Africa, the tick-bird feeds entirely on the ticks that live on the skin of large herbivores such as elephant, rhinos and antelopes. In England, starlings often pick parasites off sheep and deer. In the Galapagos Islands (which you will learn more about in Unit 21) a scarlet land-crab picks ticks off the skin of the marine lizards. In the lagoons of coral reefs, small striped fishes pick parasites off the skin of large fish of many species; the latter queue for the attention of the ‘cleaner fishes’; these live in definite places and have a very characteristic darting movement. In some other reefs, shrimps perform the same function of picking parasites off fishes. The existence of this curious niche clearly implies specialized behaviour on the part of the tick-picker and of the larger animal being cleansed of its parasites. The myriad other niches also imply specializations of structure or behaviour or both; sometimes, as with the tick-pickers, they are very ‘narrow’, but sometimes they are wide.

tick-pickers

20.2.2 The distribution of plants

Since carnivores prey on herbivores, often in a specialized way and hence on certain species of herbivore only, and herbivores eat plants, but are often highly specific and restricted in their diet to a few, or only one, species of plant, the distribution of plant species governs the distribution of animal species. The basic nutritional requirements of plants are very simple—carbon dioxide, water and mineral salts—so their distribution might be expected to be either uniform or random. But travel through different parts of the world or look at pictures of them and you will realize that the wild vegetation is different in different places. The crops also are different. Bananas grow only near the tropics, whereas apples and pears grow freely in Britain, Canada, Tasmania and New Zealand. Oranges and other citrus fruits are produced in the Mediterranean countries as well as in California and South Africa.

What are the differences between these various countries which might explain their differences in vegetation?

Differences in ‘climate’ sum up a number of differences in factors affecting plant growth and survival.

Three important factors are rainfall, daylight and temperature. Some areas have no rain for years—Arica (Chile) on the west coast of South America has an annual average rainfall of 1 mm—whereas more than 3 000 mm falls annually on others. Some places have very definite seasons—Freetown (Sierra Leone) on the west coast of Africa has an annual rainfall of 3 990 mm and more than half of this falls in the three months July, August and September—whereas in others there is rain evenly dispersed through the year. Compare these extremes with London (annual average 620 mm) and Seathwaite, Cumberland (annual average 3 290 mm, mostly falling in the winter).

rainfall

Light is essential for photosynthesis. You are aware of the change in day-length and in the intensity of sunlight in the British Isles during the year.

light

How do the day-length and intensity of sunlight vary

(a) close to the Equator, (b) in 'high' latitudes, more than 67° north or south of the Equator?

- (a) There is very little change in either day-length (about 12 hours) or the maximum intensity of sunlight (but there may be seasons with many cloudy days).
- (b) There is a contrast between mid-summer with 24 hours of daylight and midwinter with continuous night; the intensity of sunlight varies from nothing to a high level.

What differences in plant growth would you expect to find between places with equal day-length through the year and those with day-lengths varying between 0 and 24 hours?

You must be aware that most plants in the British Isles grow between about March and October—for many of them, the amount of light is insufficient for growth in the winter period. Plants growing in higher latitudes have shorter growing periods.

Of course, the changes in amount of light in high latitudes are accompanied by changes in temperature. Plants living there are subjected to long periods of freezing cold in winter, and the adverse effects of this must be added to the adverse effects of the limited growing period.

In tropical regions, great seasonal changes in rainfall may control seasonal growth of plants. Some tropical plants, however, are very sensitive to changes in day-length and respond to differences as little as five to fifteen minutes.

Thus from a study of rainfall, day-length and temperature through the year, it should be possible to predict how favourable for plant growth the conditions are in different parts of the world. Look at Figure 5 which shows the natural vegetation typical of different areas of the world (p. 24).

In the very high latitudes of the northern hemisphere is the treeless tundra, dominated by lichens. South of this is a belt of evergreen coniferous forest, and south of this are forests of broad-leaved deciduous trees (i.e. trees which lose their leaves in winter). In those parts of the tropics where there is a high rainfall, there are luxuriant forests. Between these forests and the temperate deciduous forests lie the grasslands called savannahs and steppes, and evergreen woodlands. Where the rainfall is very low or where it is very erratic and varies from year to year, there are the great deserts of the world. These vegetational zones are named after the *climax* vegetation—the natural vegetation which should grow if there were no human or other interference. Thus, in Britain, almost any area will revert to woodland if left uncultivated. Even a lake will gradually fill up with silt and turn into a marsh and then a fen and finally into woodland. In upland Scotland, the wood will probably be coniferous, but English woodland will be of broad-leaved trees.

Within the broad vegetational zones defined by climate, there are variations in the distribution of wild plant species. This can be seen even in the

When there is no light, plants must cease to grow, so plants in places with variable day-length would be likely to grow very well during the summer part of the year and stop growing completely in winter; in contrast, with no variation in day-length, the plants should grow uniformly through the year if other factors allow this.

temperature

vegetational zones of the world



Figure 5 Map to show the main vegetational zones of the world.

small area of southern England. Tansley, in his monumental work *The British Islands and their Vegetation*, describes the oak-woods as consisting typically of:

- 1 a tree layer—mainly oaks, with ash and sycamore frequently present;
- 2 a shrub layer—mainly hazel, with hawthorn, blackthorn and others frequently present;
- 3 a field layer—the botanists' 'herbs'. There are many species which may be present but not all in the same wood. Contrast these two lists of common herbs:

List A

Pteridium aquilinum (bracken)
Rubus 'fruticosus' (blackberry)
Endymion non-scriptus (bluebell)
Agrostis tenuis (grass)
Holcus mollis (grass)

List B

Mercurialis perennis
 (dog's mercury)
Urtica dioica (stinging nettle)
Circaea lutetiana
 (enchanter's nightshade)
Fragaria vesca (wild strawberry)
Brachypodium sylvaticum (grass)
Deschampsia caespitosa (grass)

oak-woods

Soil composition, texture and drainage are included in *edaphic* factors (from the Greek for 'soil'). List A is from oak-woods growing on an acid, sandy, dry soil where the shrub layer is often rather scanty; list B is from damp oak-woods growing on alkaline, clay soil where the shrub layer is usually well developed.

Look at film strip 20(b): 1, 2, 3 and 4. These illustrate the effect of the spacing of the trees on the field layer (the herbs) of a woodland.

The distribution of plants also depends on their past history and on the other species present. Each species evolved in a limited geographical area and its spread from this area depends on some mechanism for dispersal; this is often either by wind-blown seeds or by animals eating fruits. Man, the cultivator and traveller, has introduced many species into areas which they had not colonized unaided. A plant arriving in an otherwise suitable locality may fail to establish itself, either because it cannot compete with the plants already growing there or because it is eaten out by herbivores. Similarly, animal species arriving in a new locality may fail to survive, either through lack of suitable food or shelter, or because of the presence of competitors or predators. Those organisms that do establish themselves have succeeded in finding and occupying suitable vacant niches or in replacing resident species.

To sum up:

The presence or absence of a species of animal or plant depends on many factors:

- (i) whether the species reaches that particular place;
- (ii) whether climatic and edaphic factors are suitable;
- (iii) whether the appropriate food is present;
- (iv) whether the species can survive in the face of competition or predation.

Now you can do SAQs 5 to 7.

If you are a gardener, you probably realized that these herbs come from woods growing on different types of soil.

edaphic factors

dispersal

20.3 Numbers of Individuals in Populations

One of the vital activities of organisms is reproduction. The survival of a species depends on successful reproduction of individuals. Since the survival of successfully adapted species is the basis for evolution, successful reproduction of individuals is also the basis for evolutionary change. Some organisms reproduce by simple division or by the formation of buds. Only one individual need survive long enough to reproduce for the species to be perpetuated to the next generation. You should remember (Units 17 and 19) that this type of reproduction implies that all the descendants will resemble their ancestors genetically; there is no inbuilt mechanism to produce diversity. Many flowering plants propagate themselves in this way, but it is very uncommon among animals.

The great majority of animals and most plants reproduce sexually; in Unit 19 we discussed this process at the chromosomal level and showed its importance from the point of view of genetics. In most of this discussion of population numbers, and in the following section on population dynamics, we shall generally be concerned with organisms which reproduce sexually, and so with life-histories which start with a zygote (fertilized egg) and, if successful, end with the new adult playing its part in sexual reproduction, either by laying eggs or by fertilizing eggs produced by another individual.

Suppose that there is a population of five pairs of organisms (five females and five males)—if this population is to produce an offspring generation of exactly the same number of adults, what is the mean number of eggs that each female must produce?

But you learnt in Unit 19 that there is generally an over-production of individuals in each generation. Look at Table 1 which shows the average number of fertilized eggs produced in their lifetime by females of different organisms (this is called *fecundity*). Answer the following question:

For each population to remain stable (i.e. for the number of adults in the offspring generation to remain the same as in the parent one), how many eggs from each female (on average) must survive?

For each species, write down the number of eggs which must die before becoming adult, if the population is to remain stable. Then express this number as a percentage of the total number produced.

The last set of numbers you have written down are called the *pre-reproductive mortality* for each generation. The word *mortality* is used to measure the 'rate of death'—the percentage dying (in this case between egg production and reproduction of adults of the next generation). Subtract this figure from 100, to measure *survival* for the same period. Thus, for penguins the survival to the reproductive stage is $100 - 75 = 25$ per cent; for mice it is $100 - 96 = 4$ per cent. The fecundity, when expressed

Table 1

Average number of fertilized eggs produced by each female

oyster	100×10^6
codfish	9×10^6
plaice	35×10^4
salmon	10×10^4
stickleback	5×10^3
winter moth	200
mouse	50
dogfish	20
penguin	8
elephant	5
Victorian Englishwoman	10

Assuming that every egg is fertilized and that every egg grows into an adult, then the number is two. In producing two eggs each of which grows into an adult, the female is providing a replacement for herself and a replacement for one male.

Two.

e.g. penguin—6 must die if only 2 can survive: $6/8 = 75$ per cent.

as a proportion of the adult population (this is called birth rate when applied to mammals), measures the inherent ability of the population to increase. The pre-reproductive mortality measures the rate of death of a generation.

What is the relation between fecundity and pre-reproductive deaths if the population is stable (numbers of the offspring generation able to reproduce = numbers of parent generation)?

Fecundity minus deaths should equal the number in the parent generation.

If (births minus deaths) > than parent numbers, there will be more individuals in the offspring generation than in the parent generation. If this is repeated for several generations, the population will keep increasing exponentially.

Conversely, if (births minus deaths) < parent numbers and this state of affairs persists for several generations, then that population will keep on decreasing.

If you need to convince yourself of this, turn to SAQ 9.

Usually the death rate is more variable than the birth rate. Thus, changes in the numbers of breeding adults are generally a result of changes in mortality; so, in most of what follows, we shall be concerned with factors causing mortality.

birth rate and death rate

In the discussion so far, we have taken as the unit of time 'a generation'—that is, the interval between the production of eggs by parents and offspring. Table 2 shows that this varies greatly with species and may vary with external factors such as temperature. In practice, times are generally measured as recorded by clocks and calendars, but it is very important to interpret these from the biological point of view in relation to the duration of each generation.

Table 2

Average generation times for various species

Species	Generation times (averages)
man	20 years
elephant	20 years
royal albatross	10 years
codfish	6 years
salmon	4 or 5 years
great tit	1 year
stickleback	
winter moth	
mouse	8 weeks
Drosophila (fruit fly)	3–4 weeks

We have rather assumed so far that generations are discrete—that is, the lives of the parents and offspring scarcely overlap in time. This is the rule for thousands of species of British insects that have an annual life cycle. Take as example the winter moth: this gains its name because the adults are active in November and December. The males have normal wings; they fertilize the eggs as the wingless females climb up the trunks of oak-trees by night. The eggs are laid on the oak twigs and the adults die; the eggs hatch in spring, in March or April, into green caterpillars; these feed on the oak leaves and when full grown, usually in May, let themselves down to the ground on silken threads. They burrow into the ground and each forms a chrysalis or pupa from which the adult emerges on a 'warm' night in the following November. Since the adults die after the eggs are laid, there is no overlap between the active adult and the next active stage, the caterpillar; each generation takes one year.

winter moth life history

Look at film strip 20(c) for photographs of winter moth adults, caterpillar and pupa. The life cycle is illustrated in Figure 8 (p. 33).

For many other species of insects, and for most fishes, birds and mammals, the generations overlap. Adults may produce several separate broods of offspring and their older offspring may breed while the parents are still breeding. Take as example the domestic cat.

If a female cat produces her first litter of kittens when she is exactly one year old and her offspring behave in exactly the same way, how many generations of her offspring could be alive in the month before she reaches her seventh birthday?

An analysis of a cat population with overlapping adult generations and a long adult life is clearly more complicated than an analysis of a winter moth population with discrete generations and an annual life cycle. This explains why most of the examples we shall use in discussing population dynamics are studies of insects (these are also important because they are 'pests').

Pre-reproductive mortality covers all the deaths from whatever causes between the laying of a batch of fertilized eggs and the maturation of the surviving organisms which emerge from them. Some eggs may die before hatching and individuals may die at all ages between hatching and maturity. Thus there will be a decrease in the number of survivors with time; when plotted on a graph, this is called a *survivorship curve*.

Mother cat's birthday	Offspring new born	Generations adult
0	—	—
1	first	—
2	second	first
3	third	first and second
and so on:		
6	sixth	first to fifth

So the answer is that six generations of offspring could be alive just before the mother cat's seventh birthday (and she could well still be breeding herself and producing three litters a year!).

Which of the three descriptions refers to each of the survivorship curves of Figure 6?

- (a) There is high mortality soon after the eggs hatch and thereafter the numbers fall off gradually; some adults live for several years.
- (b) There is high mortality soon after eggs hatch; the adults live for a few days only.
- (c) The numbers fall off gradually until near the end of the life span, when the adults begin to die in large numbers.

- (a) describes the curve for the trout;
- (b) describes the curve for the winter moth;
- (c) describes the curve for man.

Many species of animals suffer a high mortality early in life (like the trout). When there are marked changes in body form, as in winter moth (or when tadpoles change into frogs), there are often also periods of high mortality. Survivorship curves form the basis for tables of 'life expectancy' such as those used by actuaries computing rates of human life assurance.* These

* See Table 2 (p. 10) of Population Dynamics, by M. E. Solomon, for a human life table (for the U.K.). Figure 3.1 on the same page shows three survivorship curves.

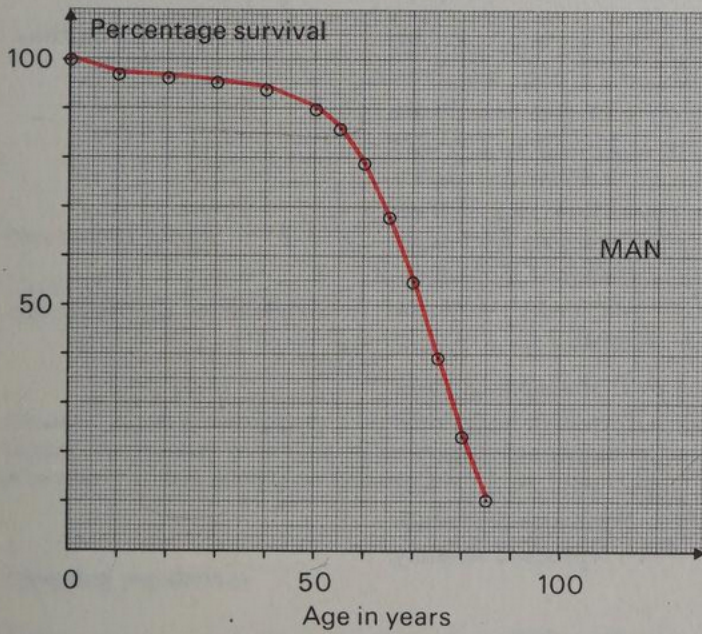
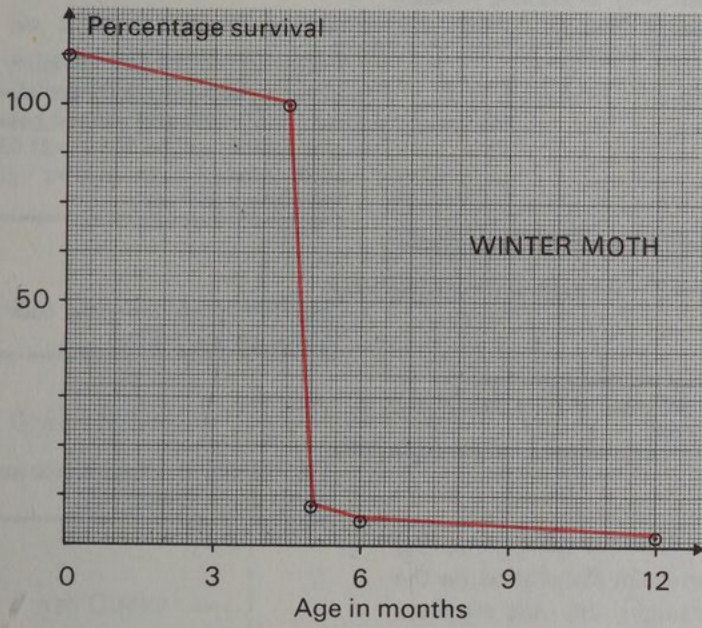
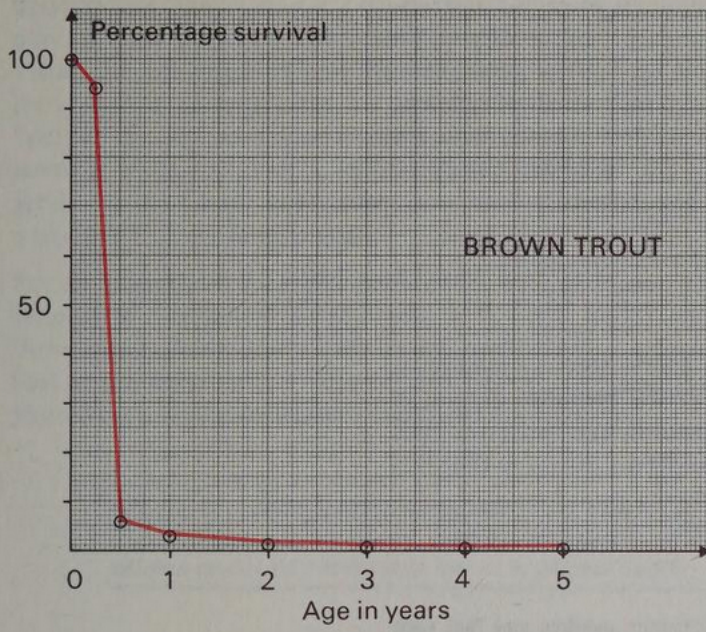


Figure 6 Survivorship curves for three organisms.

tables give the mean expectancy of life for individuals of each age. Constructing such life tables is an essential step in the investigation of population dynamics (see later). They make it possible to deduce 'age-specific mortalities'—that is, the rates of death for groups of individuals of different ages (or at different stages of the life cycle). Knowing when individuals are most likely to die makes it possible to identify the important causes of death and thus the factors affecting the size of populations.

20.3.1 Population curves

First let us consider what is likely to happen when a species colonizes a new and initially favourable environment. When a bacterial culture is inoculated* on to an appropriate culture medium, the bacterial cells multiply through each cell dividing into two daughter cells (note that this is asexual reproduction).

Assuming that 50 cells are introduced into a culture medium and that each cell proceeds to divide into TWO daughter cells every 20 minutes, calculate how many cells are present after: 1 hour, 3 hours, 24 hours.

There are 3 divisions every hour. After 1 hour, the 50 cells will have increased to $50 \times 2^3 = 400$ cells. After 3 hours, the number will be $50 \times 2^9 = 25\,600$ cells. After 24 hours, number will be $50 \times 2^{72} = 2.35 \times 10^{22}$.

You have met a term which describes this type of regular increase in numbers—name it.

Exponential increase—refer back to Unit 2 and see *HED*.

If you were to plot the numbers of bacteria for the first three hours on an arithmetic scale and on a logarithmic scale, would either of these plots give a straight-line relationship between numbers and time?

Yes, the plot on a logarithmic scale would give a straight line.

Look at *Population Dynamics*, p. 12, Figure 3.2. Data for the exponential increase in numbers of a small mite that lives in grain are plotted on the two types of scale. Figure 3.2 (b) is almost a straight line—the numbers are plotted on a logarithmic scale.

Since the bacterial culture must be in a vessel of limited size, and the amount of medium present is limited, there must come a stage when the numbers present cannot be doubled every twenty minutes—the individuals are 'competing' for the limited 'resources' of space and medium. The rate of increase must fall off. More than 100 years ago Verhulst derived an equation to describe the rate of growth of a population in a limited environment, assuming that the resources can support a certain maximum density. When plotted on an arithmetical scale, the numbers of individuals in such a population give a curve called the 'logistic curve'—look at Figure 3.3 (p. 15) of *Population Dynamics* for an example.

logistic curve

About 50 years ago, Pearl showed that numbers of yeast in a sugar solution followed the logistic curve. The same type of increase occurs when algal cells (such as diatoms) are added to an appropriate culture medium; it probably also occurs in temperate and arctic lakes and oceans when phytoplankton begins to 'grow' in spring. All these organisms reproduce by each cell dividing into two. When organisms which reproduce sexually

* Transferred from a stock culture, e.g. on a loop of wire or in a sterilized pipette; both methods were shown in TV 17.

and produce many young at a time enter a new environment, their numbers may increase in a way that resembles the logistic curve, but usually the values do not stay constant after reaching the highest value. Typically there are fluctuations, often about a slightly lower level. One example of 'natural' conditions under which organisms may colonize new environments is when pest insects, such as flour beetles and moths, reach stored products; there have been many observations and experiments on these pests, particularly flour beetles.

fluctuations in natural populations

For an example of a natural community, look at Figure 7 for population changes of caterpillars on oak-trees in Wytham Wood near Oxford. All these species have annual life cycles with discrete generations, and all feed at the same time of year on oak leaves. Note that the numbers are plotted on a log scale. Answer the following questions:

What is the proportion between the lowest and highest numbers for: winter moth; green tortrix; November moth? Do the numbers of the caterpillars of different species vary in the same way or in different ways?

So, when we discuss population dynamics in section 20.4, we shall try to explain why some organisms are common and others are rare, as well as trying to explain why the numbers of individuals of all species fluctuate from year to year (generation to generation).

All the values fluctuate in roughly the same way—there are years when all the caterpillars are numerous, and years when all are few; the ratio between maximum and minimum numbers recorded is roughly 100 to 1 for all the species, but some species are always more numerous (i.e. these are common) whereas others are always less numerous (these are rare).

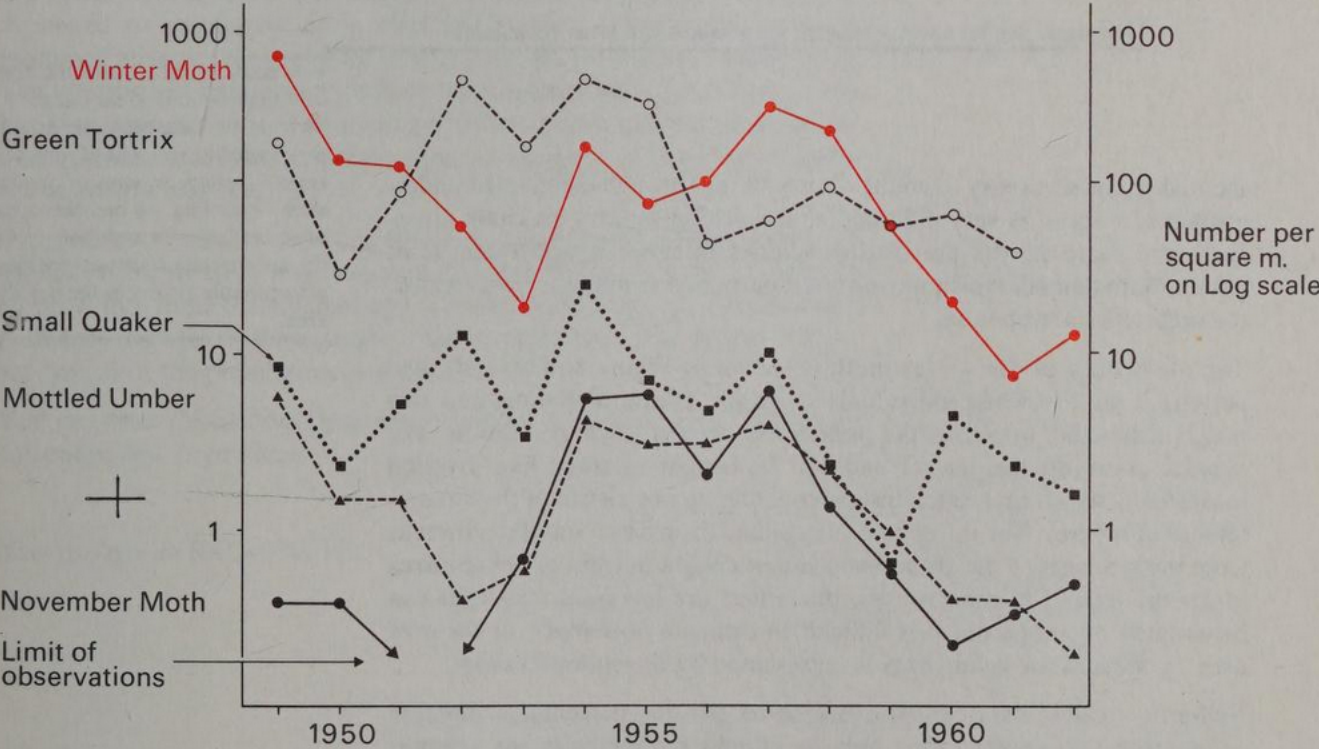


Figure 7 Population changes for some caterpillars on oak-trees in Wytham Wood, near Oxford. The numbers are plotted on a log scale. See film strip 20(c): 3, 6, and 7 for photographs of three of these caterpillars.

20.3.2 Sampling populations

Laboratory experiments are set up so that all the individual organisms can be counted and perhaps measured at various stages. Thus, accurate figures

are obtained for the changes in number and size and shape of individuals during the course of the experiments. Even so, in replicates (repeats) of the experiment, using organisms of the same species, same population, even of the same family, the figures are very unlikely to be identical. In your first home experiment, you found that physical measurements are not exactly accurate. Here we are dealing with biological material of great complexity (whole organisms) so it is not surprising to find some variability. There are now many statistical tests available for assessing whether the differences between observations are significant or could have arisen by chance.

The same problem of inherent variability must arise in field investigations comparing, say, the caterpillar population of two adjacent oak-trees or in two separate woodlands. A further difficulty in field studies is the improbability of collecting and examining every single organism in the population. Indeed, such a procedure might disrupt completely the natural sequence of events. So estimates of natural populations are based on *samples* (like public opinion polls).

population estimates

There are many published papers on methods of collecting organisms and making such collections quantitative; there are statistical tests and computer programmes for deducing from a sample the probable size of the population from which it came, and for obtaining the probability of this being a reliable estimate. The methods used must be related to the habitat being studied and the life-history and behaviour of the organisms under observation. Consider first a plant community growing on the chalk downs:

How would you set about estimating the numbers of a given plant here?

Rooted plants seem easy to count—but walking through the tangled undergrowth of a forest is very different from marking squares on chalk grassland, and there can be practical difficulties in carrying out a census of plants. With animals which move about, perhaps avoiding the investigator, the difficulties are obvious.

You could crawl all over the downs, counting the individual plants—perhaps marking each one on a map. But probably you would sample certain areas—perhaps squares of one metre sides—counting the number in each of several squares and then applying the appropriate statistical method to get probable estimates for the whole area.

The life-history of the winter moth is shown in Figure 8. There are two periods in its life when individuals move in definite directions and this makes it possible to census the population twice in each generation. The females crawl up tree-trunks and can be caught in traps like inverted lobster pots which each catch insects crawling up one eighth of the circumference of the tree. The full-grown caterpillars drop down on silken threads from the branches to the ground and can be caught in trays of definite area under the trees. For other stages, the counts are less accurate—eggs can be counted on twigs, but it is difficult to estimate how much of the area used by females for laying eggs is represented by the collected twigs.

Full-grown caterpillars can be dissected to give the percentages diseased or attacked by parasites. One parasite attacks the pupae in the ground; adults of this parasite and of others can be collected by inverting a metal tray of known area with glass tubes fixed in its corners. The adult parasites go towards the light and therefore collect in the tubes. The numbers collected give a value for density of parasites related to the ground area; the percentage of pupae attacked can then be derived from the known numbers of larvae which descended over that area of ground. These population estimates all assume that the sample areas are typical of the whole area and it is essential to calculate limits of probability using statistical methods.

winter moth census

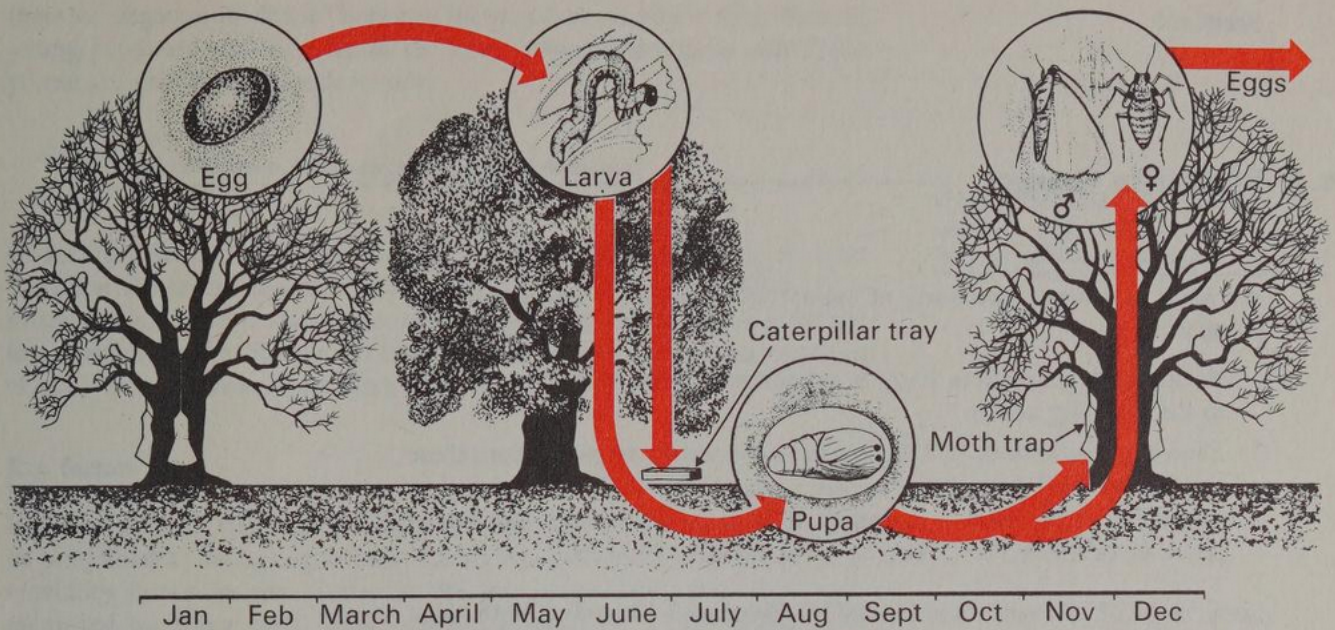


Figure 8 The life cycle of winter moth and methods of sampling its population. See film strip 20(c): 2 and 3 for photographs of live winter moth adults and caterpillar; and 20(c): 4 and 5 for parasites of winter moth and empty pupal cases.

For each species studied, special methods of trapping must be devised to be used in appropriate places and at appropriate times. Small mammals such as voles and fieldmice are caught in box traps; birds may be caught in traps or in mist nets or persuaded to use nest-boxes; fish may be trapped or netted or caught by using electrical gadgets. The animals may be examined alive and then released or may be killed for detailed examination. The recapture of animals which have been marked and released forms the basis for some methods of estimating populations; the subsequent examination of animals caught on previous occasions gives positive information about growth and survival.

Populations of animals with long lives and overlapping generations present special problems since it is desirable to break down the total population numbers into those for different age or generation groups. So it is necessary to deduce the ages of the animals in the samples and to assume that these are typical of the population as a whole.

You can read *Population Dynamics*, chapters 1, 2 and 3 as a black-page Appendix now if you like.

Now you can do SAQs 8 to 11.

traps

20.4 Population Changes

We have mentioned two sorts of change in number of individuals in a population:

- 1 Within each generation, there is a reduction in numbers from the eggs to the breeding adults.
- 2 There are fluctuations in numbers from generation to generation; these can be revealed by counts of the same stage of the life-history in successive generations—i.e. counts of caterpillars over a number of years, or of moths, or of kittens, or of five-year-old cats.

Look at p. 17 of *Population Dynamics*. Figure 4-1 illustrates both these types of changes, using data for a grasshopper population. Figure 4-2 shows the second type of fluctuation in numbers, based on counts of the pupae of a moth; note that the full line is for the actual counts of pupae per 100 m², and the dashed line shows the same numbers plotted on a logarithmic scale.

Fluctuations in numbers from generation to generation could depend only on breeding success of the adults—on the number of eggs that the average female is able to produce. This situation may operate for species of birds with special nesting sites. If all available sites are occupied, then no further females are able to lay and incubate eggs; thus the number of nesting sites sets a maximum limit to the number of eggs. If the generation suffers little mortality, then there will be an excess of birds over sites. The number of nests will be the maximum possible and some birds will be unable to breed. If there is heavy mortality within the generation, then there may be unoccupied nesting sites, and egg production will be less than the maximum possible.

Many birds show territorial behaviour during the nesting season. Each pair, or sometimes only the male bird, reacts in a characteristic 'threatening' way to any other bird of the same species which enters the area round the nest; the intruders usually retreat at once. The threat may be expressed by a gesture, such as the display of the robin's red breast, or by song, or in both ways. Sometimes the territory is just a nesting area and it may be very small, as is that of gulls in their crowded breeding colonies; but often the territory is also the area in which the parent birds find the food for themselves and their young. The system of territories spaces out the breeding pairs, setting a maximum limit for any area. Usually the territories vary in size; they are smaller when the potential breeding population is large and larger when this population is small. Other animals besides birds also display territorial behaviour, for instance, such fish as the male stickleback.

territory

The degree of crowding of the adults may also affect reproductive success. When voles* are crowded together, the females produce on average fewer young than when they are not so crowded. This is an example of an effect which is 'density dependent'. If the average number of young produced are plotted against the degree of crowding of the adults, there is an inverse correlation between the two. See Figure 4-8 (p. 21) of *Population Dynamics* for similar figures for a great tit population. For the voles and the tits,

crowding

* Voles are herbivores resembling mice.

there is 'negative feedback' between the numbers of adults and those of young produced: an increase in the adult population means that fewer young are produced by each female.

What will happen if the population of adults decreases?

The average number of young produced per female will increase and the population will rise again.

So far the discussion has assumed that pre-reproductive mortality remains the same whatever the size of the population; but, as stated earlier, most investigations have revealed that changes in fecundity (or birth rate) are less dramatic and probably less important in population fluctuations than changes in death rate (mortality).

0.4.1 Key factors

Haldane showed that calculations involving mortality and survival can be simplified by using logarithms. He represented the killing power of a mortality factor by the change in the population density caused by it measured on a log scale. This logarithmic measure of killing power is termed the *k*-value; it expresses the reduction in numbers of individuals, per unit area, caused by one mortality factor.

k-value

The total pre-reproductive mortality, *K*, is the sum of the killing powers of the mortality factors acting in succession on the population of eggs produced by the parent generation. Thus,

$$K = k_1 + k_2 + k_3 \dots k_n.$$

Each *k*-value is the difference between the logarithms of the numbers of individuals per unit area before and after its action.

Take the winter moth as an example. Refer to section 20.3.2 if you need to remind yourself about its life-history (shown in Figure 8, p. 33) or the methods used to sample its numbers and those of its parasites. Suppose that the population is not changing, so that the number of breeding adults per unit area is the same for the parent and offspring generations. Let us consider the offspring of a single female as occupying unit area.

Then, if each female produces 200 eggs, what is the value of *K*?

Here is a table for the winter moth, showing the average number of individuals killed by six mortality factors acting in succession:

Of these 200 eggs, only 2 can survive so:

$$K = \log 200 - \log 2 = 2.3010 - 0.3010 = 2.0$$
$$\text{or, } K = \log \frac{200}{2} = \log 100 = 2.0$$

Number of eggs laid by female moth	200
Number killed by 'winter disappearance'*	184
Number of caterpillars killed by a parasitic fly	1
Number of caterpillars killed by other parasites	1.5
Number of caterpillars dying from disease	2.5
Number of pupae killed by predators in the soil**	8.5
Number of pupae killed by a parasitic wasp	0.5
Number of adults surviving to breed	2

Film strip 20(c) includes photographs of the fly (number 4) and the wasp (number 5).

* 'Winter disappearance' includes the eggs dying from all causes (probably a small number), and a heavy mortality of young caterpillars directly after they hatch from the eggs.

** The pupae in the soil are eaten by various beetles and by shrews.

From these figures for winter moth, the following k -values are derived:

k_1 = the killing power of 'winter disappearance' = 1.10

k_2 = the killing power of the parasitic fly that attacks the caterpillars = 0.03

k_3 = the killing power of other parasites that attack the caterpillars = 0.04

k_4 = the killing power of the caterpillar disease = 0.09

k_5 = the killing power of predators that attack the pupae = 0.64

k_6 = the killing power of the parasitic wasp that attacks the pupae = 0.10

Total pre-reproductive mortality = $K = k_1 + k_2 + k_3 + k_4 + k_5 + k_6$ = 2.00

Since we have used average values, $K = 2.00$ and the offspring generation of adults would equal in numbers the parent generation; the population would remain constant. Look back to Figure 7. The numbers of caterpillars of winter moth fluctuate greatly from year to year; this suggests that K fluctuates. If this is so, then at least one k -value must fluctuate.

winter moth k -values

Figure 9 shows how K and the successive k -values varied between 1950 and 1961.

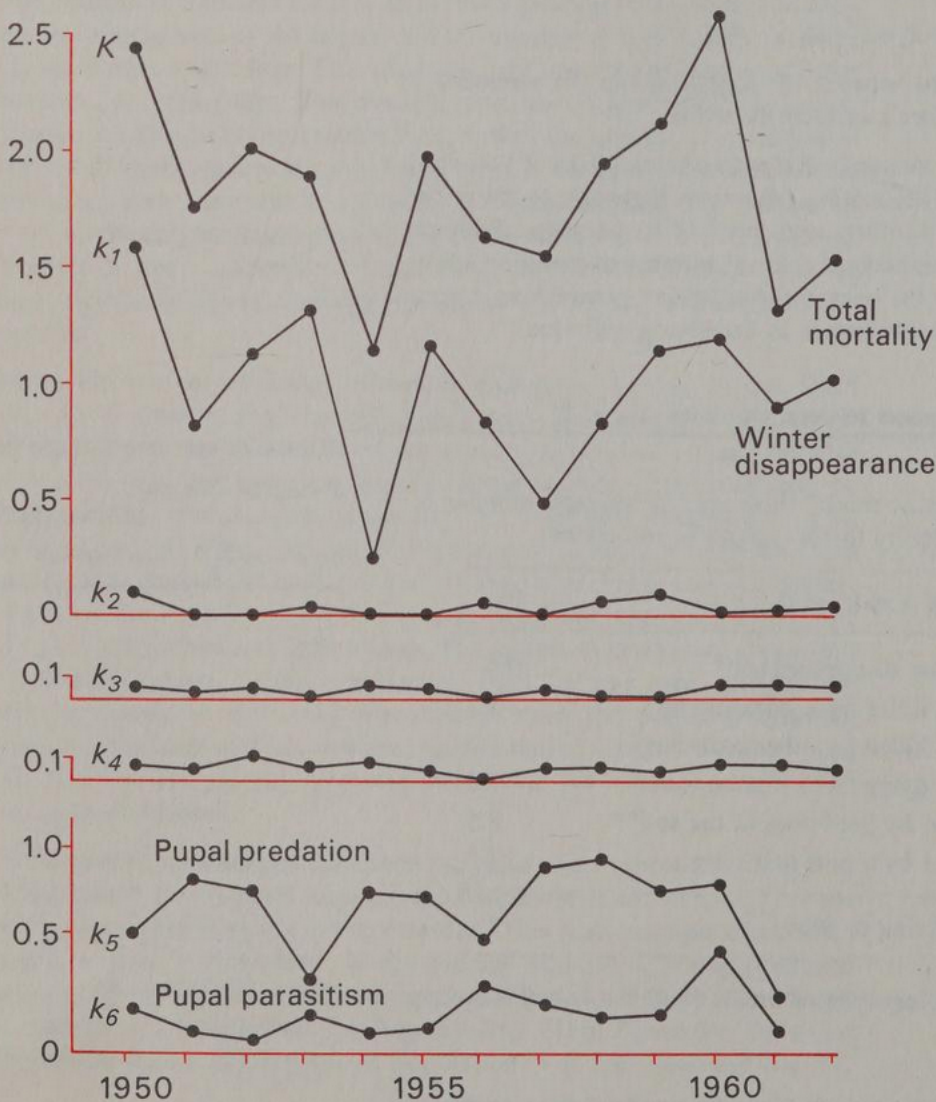


Figure 9 K and k -values for winter moth in Wytham Wood between 1950 and 1961.

It is obvious that the values for k_1 (winter disappearance) fluctuate in almost exactly the same way as the values for K (total mortality). This means that changes in k_1 account for almost all the change in K from year to year so k_1 (winter disappearance) is called the *key factor*. It is the major cause of the enormous fluctuations in the numbers of winter moth caterpillars. Although part of this mortality may be due to death of eggs, most of it occurs because the very young caterpillars do not establish themselves and start to feed. The eggs hatch in spring at about the time that the buds of the oak-tree open and its young leaves begin to grow. If the caterpillars hatch before the buds burst, they starve. As a result of natural selection, the hatching time of winter moth eggs is almost synchronized with the bud burst of oak-trees; but slight differences in timing lead in some years to very successful establishment of caterpillars and consequent defoliation of the oak-trees and in other years to high mortality of young caterpillars. You may wonder why the hatching time is not delayed—probably, if the caterpillars hatched too long after the buds burst, there would be a mortality later, because the leaves become tough and loaded with tannin, and many caterpillars would fail to reach the stage of being ready to pupate. So there would be selection against later hatching.

caterpillar survival

0.4.2 Regulating factors

Winter moth numbers fluctuate about a mean level. Figure 9 shows that changes in k_1 are usually greater than changes in K : this suggests that some other factor compensates by reducing the numbers more when k_1 is small and less when k_1 is large. This compensatory effect must be density dependent and it is acting as a *regulating factor*. There is negative feed-back, restoring the status quo.

density dependent factors

Try to identify possible regulating factors from the graph of k -values for winter moth.

To make a convincing case for a certain mortality factor to be a regulating factor, it is necessary to show that its values vary in the appropriate way with the winter moth density to an extent that is statistically significant. This requires data from the same place for a number of years and it also requires a good understanding of statistical theory. For the winter moth, k_5 (pupal predation) is density dependent: when there are large numbers of pupae in the ground, then the predators prey on them more heavily. It appears that they concentrate on winter moth when it is abundant, but tend to ignore it when it is scarce. Thus the activity of the predators tends to stabilize the numbers of winter moth.

There are two possible regulating factors: pupal predation and pupal parasitism. No other k -values show consistent relationship to K .

The pupal parasite is an ichneumonid* wasp. Many ichneumonids are parasites of insects. In this Unit's TV programme you will see one that is parasitic in flour-moth caterpillars. Most are highly specific, being able to live only on individuals of one host species. Although they are generally called parasites, they kill and usually consume the whole of the host, so that they are as much specific predators (each slowly consuming only one individual) as parasites in the usual sense of that word. The fly that parasitizes the winter moth caterpillar is also this type of parasite. The part played by such specific parasite-predators in population control is of special interest, because, if successful, they can regulate the numbers of their host species while having no direct effect on any other organism.

insect parasites

* A special type of wasp with larvae that are parasites of other insects.

There have been various theories and mathematical formulations to explain the interrelationships of insect host and insect parasite. Probably these parasites act as *delayed density-dependent factors*—that is, their reproductive rate depends on host density so that their own numbers are one or more generations out of phase with the host numbers. When numbers of hosts are high, the parasite is successful and the following year there will be large numbers of parasites. If the host is still plentiful, the percentage attacked by the parasite will be larger, because of the large number of parasites, so the host numbers will be reduced. The large generation of parasites emerging the following year will find fewer hosts to attack and so they will be less successful; the following year the parasite numbers will have fallen.

delayed density-dependent factors

In Figure 7, the numbers of different species of caterpillars can be seen to change from year to year, but some, such as the winter moth, are always common whereas others, such as the November moth, are always rare. The fluctuations from year to year are caused by variations in key factors. It is possible that all these species of caterpillar have similar key factors; their numbers fluctuate in roughly the same way. The difference in average population numbers of common and rare species depend on the regulating factors. It is obvious that regulating factors act so that November moth numbers never exceed 10 m^{-2} whereas winter moth numbers vary about an average of about 100 m^{-2} . If winter moth numbers are sufficiently high for trees to be defoliated, it clearly becomes a 'pest'. Since this cannot happen if the regulating factors act to maintain small population numbers, it is of economic interest to be able to identify these factors. It may then be possible to manipulate them so that the insect becomes or remains rare: then it cannot become a pest. See 20.6.1 for a discussion of pest control.

rare and common species

20.4.3 Population models

The ultimate test as to whether key factors and regulating factors have been identified correctly is to simulate the inter-relationships by calculation, starting with the actual numbers counted in a certain year, inserting the various factors operating at the levels required by the current theory and then working out how the numbers should vary through the following years. The calculated figures can then be compared with those actually observed in the field.

This test has been applied to the winter moth at Wytham (see Figure 10). Starting with the observed value for winter moth caterpillars in 1950 and using each year the actual k -value for winter disappearance (since so far there is no method of predicting this from other observations), but representing the k -values for pupal predation by a density-dependent factor and using constant values for the other k factors, calculations resulted in a set of figures which are not very far from those observed. Adding a k -value for parasitism, which varied as suggested by theory, improved the fit of the computer values in relation to the observed values. A new interpretation of the relation between parasite and host density and a consequent adjustment in the appropriate k -values has led to even better correspondence of observed and predicted values. From these new relationships, curves for the numbers of parasites to be expected were derived, and these vary in the same way as the observed values. This makes it very probable that the key factor and regulating factors for winter moth in Wytham Wood have really been identified and the latter accurately quantified.

The new interpretation of host-parasite relations was formulated from observations of the behaviour of an ichneumonid parasite called *Nemeritis*, whose host is the caterpillar of the flour moth. You will see flour moth caterpillars and adults of *Nemeritis* in this Unit's TV programme. In a

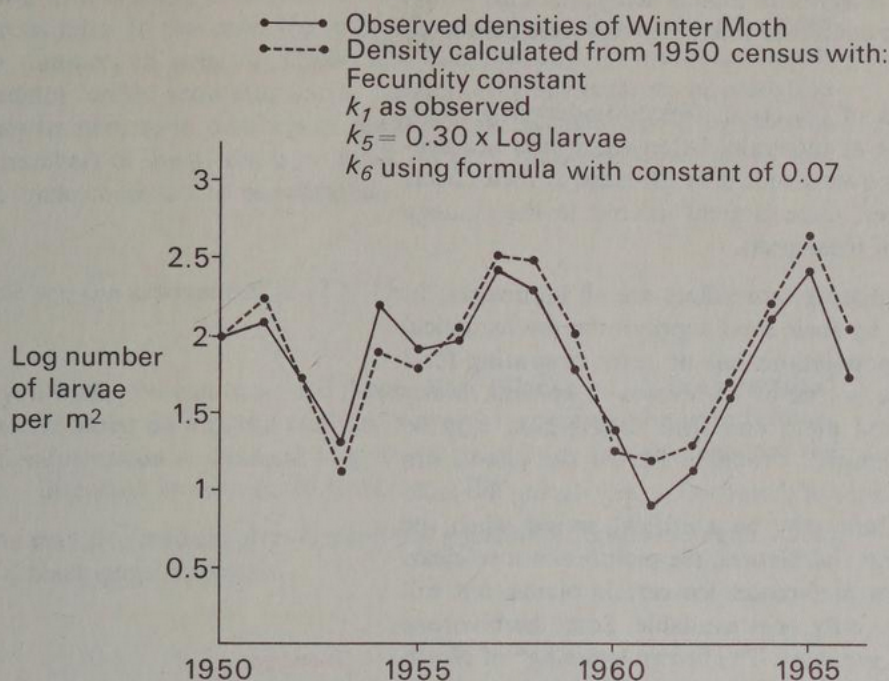


Figure 10 Observed and calculated densities of winter moth in Wytham Wood. The calculated values were obtained by starting with the value for 1950, then: assuming constant fecundity; using the observed values for each year for k_1 ; taking k_5 as $0.30 \times \log$ number of larvae; and calculating k_6 from a formula with a constant of 0.07.

series of long-term observations on the relative numbers of host and parasite, it was found that the efficiency with which *Nemeritis* killed caterpillars decreased as the density of the parasite increased—the more numerous the parasites in a given area, the less effective was their infection of readily available hosts. Before these observations were analysed, it was assumed, because there was no reliable data, that the efficiency of parasites in killing their hosts would depend only on the host density and would not be affected by the density of the parasites.

Parasites such as *Nemeritis* seek out areas where there are many caterpillars rather than areas where caterpillars are few. They can discriminate between caterpillars that are already parasitized and those that are free of parasites or have been parasitized for less than ten minutes. They do not lay eggs in those already parasitized. These two types of behaviour should improve the efficiency with which *Nemeritis* attacks its host, the flour moth caterpillar. When many parasites gather in the same area, the later arrivals tend to fly away when they encounter parasites already there; the parasite that flies away may find another group of hosts, so the behaviour could improve the efficiency of the parasites' attack. If the parasites are very crowded, however, there may be no groups of hosts free from parasites and their response to mutual interference then means that the parasites' attack is less effective.

Apart from its purely intellectual value in explaining observed data, a model should be able to predict what changes will occur when factors are manipulated.

Winter moth has become a pest of forest trees in eastern Canada. It had no parasites there, so one of the European parasites (the fly that attacks the caterpillar) was introduced. Winter moth numbers were reduced to low levels within five years. The population model developed at Oxford has been used to predict the likely further effects of this introduction—it predicts that there should be cyclic variations in numbers of winter moth and its parasite such that the trees should be defoliated (because of very

host parasite relations

winter moth in Canada

large numbers of caterpillars) at intervals of nine or ten years. This would be an improvement on the earlier condition when the trees were defoliated almost every year.

There are various other records of insects in forests undergoing cyclic fluctuation and defoliating trees at intervals. Often the cycles are synchronized and defoliation occurs over a wide area. Because of their effects on the growth of valuable timber, there is great interest in the strategy necessary to limit the numbers of these pests.

Winter moth and the other defoliating caterpillars are all herbivores. In most years they are not limited by their food supply—the mathematical model simulating winter moth populations has no term measuring food supply. You may wonder if this is true of herbivores in general. Many of these are specific in their food plant and their distribution may be limited if that of the plant is limited. Probably few of the insects are limited in numbers by the abundance of their food supply during the main feeding period, but for many there may be a critical period when the young first begin to feed. For larger herbivores, the picture is not so clear. Grazing mammals certainly show preferences for certain plants, but will usually eat others if they are the only ones available. Some herbivorous mammals show regular cycles in numbers. The brown lemming* of North America builds up its populations every four years. The peak numbers are followed by a ‘crash’ to minimum numbers, and the populations then build up again to another peak. Investigations have shown that peak populations eat out their food supply and the crash allows the plants to recover. The European lemming has a similar four-year cycle in Scandinavia; this is well known because during the peak periods, swarms of lemmings migrate across country, swimming over rivers and often plunging to their deaths by drowning in fjords.

lemmings

20.4.4 Predator-prey relationships

The capture of the first meal is a critical stage for many predators; once the young animal has established itself where there is a source of food, its expectation of life is markedly increased. This has been shown, for example, for ladybird (beetle) larvae, which feed on aphids (greenfly) and for young brown trout, which eat shrimps and aquatic insect larvae. Some predators are specialists, as the ladybirds are on aphids, or mammalian ant-eaters are on ants and termites. Many predators, like the brown trout, have a fairly wide food range and can change their basic diet to take advantage of any suitable organisms that are abundant.

The maximum numbers of predators in an area must depend on the numbers of prey available. If the numbers of prey fluctuate, then it is very likely that the numbers of predators will also fluctuate. The changes in numbers of lemmings in Arctic areas, described in the last section, are associated with changes in the numbers of the Arctic fox which prey on lemmings; when lemmings are scarce, the foxes prey on ptarmigan and other birds, but the number of foxes falls. The snowy owl preys on European lemmings and is unable to rear young when the lemming population is low; its breeding success follows the population curve of the lemmings with their four-year cycle.

Arctic fox

snowy owl

Turn to Figure 4.3 (p. 18) of *Population Dynamics*. This shows the fluctuations in numbers of two mites (small organisms distantly related to spiders) in laboratory experiments. One mite, the prey, is herbivorous and is pro-

* Small rodents related to voles and mice.

vided with oranges as food; the other, the predator, feeds on the herbivorous mite. In this case, the increase in numbers of the predator causes the numbers of prey to 'crash' and consequently the numbers of the predator 'crash' soon afterwards. Reduction in the pressure of predation leads to increase in numbers of the prey and this is followed by increase in numbers of the predator; a 'crash' of prey numbers soon follows and the cycle continues to be repeated.

Now you can attempt SAQs 12 to 13.

If you wish, you can now read Appendix 1 (Black), which is a structured exercise based on a recent study of a tawny owl population near Oxford. The information is arranged to give you practice in applying some of the ideas discussed in sections 20.1, 20.3 and 20.4.

You may also read chapters 4, 5 and 6 of *Population Dynamics* as equivalent to a black-page Appendix.

20.5 Changes in Communities

In the preceding four sections, we have studied the structure and size of communities in terms of food supply and niches. Communities have an ordered structure and alteration of any part of this may have surprising effects. If we knew and could quantify all the factors affecting each species, then it should be possible to devise a computer programme which could be used to predict the effect of any change in any of these factors. Our present knowledge is very far from this ideal.

We know that communities change with time—this is called *ecological succession*. Take European lakes as an example: as a result of erosion of the valleys in which they lie, and deposition of the silt carried in inflowing streams, lakes gradually become shallower. The phytoplankton species change and, as the area of shallow water enlarges, the rooted plants increase in numbers and change in species. Eventually the shallow water turns into swampy marsh, shrubs begin to grow among the rushes, sedges and rank grasses, and finally, if left to itself, the lake basin turns into woodland. As the environment and plants change, so the animals change. The fishes of deep, rocky mountain lakes are trout and char, those of shallow, silted lakes are bream, tench and their relatives; marsh animals are different from those of lakes and woodland animals different from those of marshes.

ecological succession

This phenomenon of ecological succession is a natural process by which communities change gradually until they turn into the *climax*—the typical final community characteristic of that area. This may take thousands of years. The appropriate animals and plants are able to colonize the changing area because they are already present in adjacent areas. The climax community usually has many species and niches and is more complex than the preceding ones. Because of its ecological diversity, it is usually stable. Under some conditions, there is a cyclical change from the climax back to a slightly earlier stage in the succession and then on to the climax again.

climax vegetation

20.5.1 Rabbits

Since the species within the community interact, and there is a delicate balance between them, the introduction of a foreign species, or some change in a density-dependent factor affecting a native species, may have far-reaching effects on the rest of the fauna and flora. The rabbit is a native of Europe which has been carried to many parts of the world because it is good to eat and provides a useful fur. It breeds readily in captivity and is fairly hardy, being able to survive in central Africa as well as in the rigorous climate of Tierra del Fuego. It was probably introduced into Great Britain during Norman times. It is fairly closely related to the hares, of which there are two native British species.

Historical records show that rabbits were important in English feasts in the late thirteenth century and fetched high prices; by the sixteenth century, they were clearly abundant and rabbit warrens were maintained on various estates as sources of food and fur. In 1948, the annual turnover in wild rabbits was probably between 60 and 100 million.

The first rabbits probably reached Australia in the late eighteenth century, but experts believe that this introduction was not successful and that all the subsequent rabbits in the continent were actually the descendants of only 24 wild rabbits introduced into the state of Victoria in 1859. Rabbits were phenomenally successful and spread through some two-thirds of the

rabbits in Australia

continent. Foxes were introduced (for sport) in 1868 and have also spread through much of Australia—now, with a bounty on their heads, thousands are killed each year—but they did not control the rabbits. Trapping rabbits became a considerable industry with an export trade worth several millions of pounds annually of meat to Britain and fur to the USA.

What effects did this fast-breeding herbivore have on the native organisms of the countries into which it was introduced? In Australia, the unique mammal fauna (which will be referred to again in Unit 21) has suffered greatly, both from competition with and from predation by introduced mammals such as the rabbit and fox. Rabbits also competed with the introduced sheep and cattle. With their burrowing habits, they contributed to soil erosion.

The influence that rabbits had on the environment was shown clearly when their numbers were drastically reduced following the impact of the virus disease, myxomatosis, first in Australia and later in Britain. This disease was first reported in 1898 in Uruguay, where it caused an unusually high mortality of nearly 100 per cent among the European laboratory rabbits. Much later, in 1942, it was proved that the native species of wild rabbits in South America are immune to the virus, probably as a result of long association between this species and the disease. When the disease was transmitted to a European rabbit, this had no immunity and died. Colony and field trials with myxomatosis in Australia between 1936 and 1943 were only partly successful and the disease did not spread, possibly because foxes killed the infected rabbits. Six out of seven further liberations of diseased rabbits in 1950 were also limited in their effects, but the seventh led to rapid dispersal of the disease, with mosquitoes acting as carriers. Some million square miles were infected in the first summer; the disease died down in the winter but reappeared in epidemic form in the following summers; probably 1952–3 was the peak year. In the first few years, the mortality among infected rabbits was 99.5 per cent, but this fell off to less than 90 per cent by 1955—probably due to change in the virus and the appearance of antibodies in young rabbits. There were dramatic effects on sheep production—the increase in wool production alone was worth some 34 million pounds; other increases in rural production brought the total profit to 50 million pounds.

myxomatosis in Australia

The disease was introduced into France deliberately in 1952 and spread rapidly reaching almost every part of the country in 1953, and also the Netherlands, Germany and Spain. In Britain, wild rabbits with myxomatosis were first seen in the summer of 1953 in Kent and Sussex. The method of introduction is not known, but it was not a deliberate act by anyone in authority and at first there were attempts to contain the centres of infection with rabbit-proof netting. This became impracticable as other outbreaks started and, by the end of 1954, the disease had spread almost throughout the country. In Britain the carrier is the rabbit flea; rabbits which do not make burrows and nests are much less likely to contract myxomatosis than the others.

myxomatosis in Europe

Refer back to Unit 19, section 19.6.1, for more information about the disease and changes in the virus and in rabbits.

What were the effects in Britain of the disappearance of almost the whole rabbit population through myxomatosis?

First, consider changes in the vegetation: the areas where the disappearance of rabbits has made the greatest impact are the chalk downlands characteristic of southern England. These were grazed by sheep in the Middle Ages, but in more recent times the principal grazing animals have been rabbits.

Film strip 20(b) includes two pairs of photographs: one of each pair taken before and one after myxomatosis had killed almost all the rabbits in that locality. Both are chalk areas. Lullington Heath, Sussex, was photographed in early spring and Old Winchester Hill, Hampshire, was photographed in August.

Look at film strip 20(b): numbers 5 and 6. What has changed between 1954 and 1967?

In 1954, the rabbit burrows on Lullington Heath were surrounded by broken turf; there was much bare chalk. There were bushes near the burrows—these are elder (*Sambucus nigra*), plants which are unpalatable to rabbits.

plants of chalk downland

In 1967, there was no bare chalk exposed; the area was covered by a dense sward of grass (red fescue *Festuca rubra*) and there were bramble bushes (*Rubus sp.*).

Thus there has been an obvious change in vegetation. Grass and brambles grew in 1967, where there were few or none in 1954.

Look at film strip 20(b): numbers 7 and 8. What changed between 1954 and 1956?

In 1954, there was much bare chalk 'scree'; there was much ragwort (*Senecio jacobaea*), the tall plant with yellow flowers like those of daisies.

Two years later, in 1956, most of the bare chalk had been colonized by plants, mostly grasses. The photograph shows no ragwort plants.

Suggest an explanation for the presence of ragwort in 1954 and its absence in 1956.

Ragwort, like elder, is unpalatable to rabbits, so it was able to grow in places where rabbit grazing kept down palatable species. Each ragwort must grow from seed; it normally flowers and dies in the second year of its life (it is a biennial). Ragwort seeds established themselves on exposed chalk, where the ground was scratched by rabbits. After myxomatosis, plants of other species grew over the bare chalk soil and ragwort seeds failed to establish themselves in the face of this competition.

ragwort

The plants of the chalk downland of forty years ago usually formed a community with leaves close to the ground; often they had attractive flowers (such as thyme). Absence of grazing allowed faster growing shrubs and herbs with leaves further from the ground to spring up and overshadow the traditional chalk downland plants. People who are anxious to preserve the original attractive community now work to clear the scrub of brambles and hawthorn, sometimes using mechanical mowers. In other places, sheep are being used for grazing again (at some cost!).

Secondly, the predators on rabbits—these are listed (in the *Handbook of British Mammals*) as: fox, stoat, buzzard, hawks, raven, crows, great black-backed gull, wild cat, farm and feral* cats and dogs, weasel, some owls and badger (the last three taking young rabbits and the rest taking rabbits of all sizes). Of these we shall consider only the fox.

Unfortunately, there are few good figures for fox diets before myxomatosis, but these suggest that rabbits and hares together formed more than half

fox diets

* Domestic cats and dogs which have become wild.

the mammals of the diet (unfortunately it is not possible usually to distinguish between these two as remains). A study of fox stomachs collected between 1955 and 1957 showed rabbits and hares in only about 20 per cent of stomachs; the most common small mammals were field voles, with immature brown rats next in frequency. Birds were found in nearly two-thirds of the stomachs from lowland foxes and the proportion of poultry and game birds in these stomachs was twice as high as before myxomatosis; hill foxes ate fewer birds and the occurrence of poultry and game was about the same as for earlier records. Hill foxes ate more sheep, probably often as carrion; the occurrence of these was about the same as for earlier records.

Foxes are carnivores eating a wide range of animals, including worms and beetles as well as birds and mammals; they also eat garbage and carrion. The disappearance of rabbits removed a prey species which had been an important component of their diet, but observers found no noticeable reduction in the weights, condition or breeding records of foxes in the next two years. Certainly their diets changed, but they were able to switch to other animals that were common and available, especially to field voles. Complaints of increased damage to poultry and game birds were probably justified in southern England but there is no evidence to support complaints of increased damage to sheep in hill districts.

Thirdly, competitors—the mammals most likely to compete with rabbits are their close relatives, the hares. Their habits are different: hares do not burrow, and they lead more solitary lives; but both species are herbivorous and were widely distributed. Hares are native to this country, whereas rabbits, as explained earlier, were introduced about 1 000 years ago.

Here is some information for an estate of about $8 \times 10^6 \text{ m}^2$ in the East Midlands: the first rabbit with myxomatosis was observed there in September in 1954; 1 800 dead rabbits were picked up in the eight weeks following this.

	Number of rabbits killed annually	Number of hares killed annually
Before myxomatosis	1 000 to 4 000	<10
After myxomatosis		
Winter 1954–5	0	10
Winter 1955–6	0	101

In September 1954, 62 hares were counted on the estate. In June 1955, a similar count gave 105 hares, including 9 leverets. In March 1956, at the end of the shooting season, 76 hares were counted on the estate.

Similar records have been published for estates in France. Where the annual ‘bag’ before myxomatosis was about 10 000 rabbits and between 100 and 250 hares, the numbers killed in the three years following the appearance of myxomatosis were less than 100 rabbits, but from 230 to 500 hares. The hare populations continued to increase slowly even when the number of rabbits began to increase again.

Biologists realized before 1954 that the activity of rabbits was important in determining the composition of certain communities. Enclosure with rabbit-proof netting of small areas of land was followed by the appearance in the enclosures of some plants that did not grow outside. But the almost complete disappearance of rabbits following myxomatosis led to some changes in communities that surprised most biologists. This is just one illustration of the fact that communities are in a delicate state of balance; alteration of part of the structure of a community may be followed by far-reaching and unpredicted changes.

hares

20.6 Man and the Environment

In pre-agricultural times, man ate berries and roots and killed various animals for meat. An omnivore with a wide food range can readily adapt its diet to changes in numbers or abundance of food organisms and so does not eat out any food species. The deliberate use of fire by man probably started quite early: this certainly alters community structure, favouring fast growing plants that can take advantage of devastated areas, such as rosebay willowherb, which is called 'fireweed', or plants resistant to heat and smoke. Large areas in Africa probably owe their present character to regular burning—and so do British grouse moors.

The development of agriculture implies very considerable interference with the natural environment. The climax vegetation is destroyed and replaced by a mono-culture—a field of wheat or cabbages or turnips replaces a forest of oak, ash, hazel and many other plants. The crops grown have characteristic demands on the soil. If the same crop is grown for several seasons in succession, the yield may fall off because some essential substance has been used up or because there is an accumulation of exudates from the crop plants. Such problems can be avoided by 'rotation of crops' or by adding the necessary substance—that is, by using fertilizers. We shall refer to this again in Unit 34. A very modern predicament arises from the use of fertilizers in such quantity that water draining from the land becomes charged with them, with consequent ill-effects on streams and rivers and on users of water.

From the biological point of view, agricultural practice is completely contrary to the natural development of communities. Agriculture typically involves mono-culture—areas, often of considerable extent (some forests), planted with a single species of plant in place of the climax community of many species. As a result there emerge two types of biological problem organisms: weeds and pests (though the latter term may be used to include the former).

Weeds are often opportunist plants—usually quick growing and early flowering annuals*—naturally adapted to take advantage of the 'gaps' in normal communities, where soil is exposed and there is plenty of light. Other weeds appear to have evolved in parallel with cultivated plants; they have no known 'wild' habitats. Some weeds, such as many grasses, reproduce vegetatively** and so can cover wide areas quickly. If cultivated ground is left to revert to the wild, the weeds are ultimately replaced by other plants as the stable climax community develops.

Pests are animals which interfere with man's agricultural practices. Most of them compete with man by consuming the crop (or part of it) or making it useless (as some insects affect forest trees grown for their wood). Just as weeds are wild plants taking advantages of niches provided by man, so pests are wild animals with their own niches in wild communities. Many herbivores are selective in their food requirements. A natural community with many species of plants in the same area will support many species of

agriculture

weeds

pests

* Plants that flower and die within a year of the seed germinating.

** Without producing seeds; e.g. potatoes are propagated by tubers and strawberry plants by runners.

herbivore in that area. For each of these species, there may be a problem in finding food plants at certain stages of their life cycles—these plants may be some distance apart and the animals need some form of dispersal. The herbivores are preyed upon by carnivores, some of which are very specific in their choice of food, and are attacked by parasites, which are often specific in their choice of host. In a long established community, there will be a stability in the balance between all these organisms, although they will probably show fluctuations in numbers.

Agriculture provides enormous food resources for those herbivores which share the same tastes as man. With many plants of one species grown close together, there is no problem of individuals finding new food plants at the dispersal stage. Thus it is possible for very large numbers of herbivores to build up on the crop plant. You may wonder why the predators and parasites of the herbivorous pests do not also build up in numbers. In fact, this must start to happen very often but, if the predators or parasites keep pace in their numbers with the herbivore, then the latter's numbers are always kept at a relatively low level and so by definition it is not a pest. Wherever crops have grown apparently free from pests, natural regulation must have operated. But if the parasites and predators are not fully synchronized with their prey, or have some special requirement during part of their life-history (special conditions in which to hibernate or lay eggs or rest during the midday heat), they may not be able to follow their prey into the cultivated land. Slight changes in the pattern of cultivation may accommodate the predators or, on the other hand, make it impossible for them to act as regulators. The removal of hedges may well reduce the numbers of predators, such as birds, beetles and hedgehogs, that keep the numbers of pests and potential pests at low levels in smaller fields.

A different problem arises when some animal is introduced into a new area where there is a suitable food supply. The introduced pest may lack completely its specific parasites and it may not be favoured by the local predators. Under these conditions it is able to build up large numbers without any regulation whatever. With air transport all over the world, the chances of casual introduction of new pests are much greater than in the days of steamships or sailing ships. Winter moth in Canada (20.4) is an example of an introduced pest with no natural enemies in Canadian forests.

20.6.1 Pest control

Since pests are animals present in large numbers, they clearly lack natural regulators to keep the populations at low (therefore agriculturally tolerable) levels. One approach to the problem is to try to introduce appropriate regulators—this is called *biological control*. Another approach is to use chemical substances (pesticides) to kill the pests—this is *chemical control*.

Two examples of biological control have already been mentioned in this text. Name them.

Both these examples illustrate the essential point about this method: the introduced agent (parasite, predator or disease) must be specific to the pest. If it also attacks other organisms, then the effects of introducing it are very difficult to predict and may turn out to be disastrous in other ways. This happened when the mongoose was introduced to control snakes in Haiti—having eaten out the snakes, the large populations of mongoose then turned their attention to many species of birds and mammals. This might have been predicted since mongoose are not specific

The introduction of parasites of winter moth from Europe to Canada. The introduction of myxomatosis to control rabbits in Australia and France.

in their feeding habits and will eat birds and mammals as well as snakes.

The use of chemical control is often rather similar to the introduction of non-specific predators—but has the advantage that it is easier to stop. Most pesticides are not specific to the particular pest but kill a large range of other insects. In field conditions, these other insects will probably include predators and specific parasites of the pest—that is, the natural regulators. If these have been killed completely, then the only way of controlling the pest is to continue to use the pesticide year after year. Sometimes the indiscriminate killing of predatory insects means that other herbivores, which were being regulated naturally, become pests. To have survived, these must be at least slightly resistant to the pesticide; thus a new problem has appeared which may well be worse than the original infestation for which the pesticide was used. An example of this, quoted in Unit 19, is the appearance of flies resistant to DDT.

chemical control

The case of the cottony-cushion scale in California illustrates some features of biological and chemical control. Turn to p. 48 of *Population Dynamics* and read the first paragraph of 7.3; the lower photograph of Plate 1 shows the scale and the introduced specific predator, the ladybird *Rodolia*. After the War, citrus growers started to use chlorinated hydrocarbon insecticides such as DDT. One result was the re-emergence of cottony-cushion scale as a pest in Californian orchards, since the pest seems to be much more resistant to these insecticides than is the ladybird. When the citrus growers altered their insecticide programmes, *Rodolia* was able to survive and to keep the scale under control. Note that the ladybird used to be called *Vedalia* and you may find it described under that name in some books.

biological control

While biological control is clearly an elegant way of controlling pests—and the most economical way from the point of view of running costs—it must be realized that the search for appropriate regulators may be long and may not always be successful. Insecticides are necessary adjuncts to agriculture, but it is essential that they be used discriminately and with a clear understanding of all the possible biological consequences. This has not been the case in the past. When the choice of insecticide lay between substances such as derris,* which break down quickly and are not toxic to mammals or birds, or such obviously dangerously poisonous substances as arsenates or lead salts, the use of insecticides did very little real damage to the environment. The situation was changed by the development of DDT and related compounds. These are very effective and persist for long periods in the soil, so they appeared at first to be ideal as agricultural pesticides. It was some years before it was realized that they act as cumulative poisons in birds and mammals and are passed along the food chain and so accumulate in carnivores. The battle to restrict the use of these stable, persistent pesticides is still raging; you should find it of interest to read *Silent Spring*, the book by Rachel Carson that first made the general public aware of the very dangerous situation arising from the indiscriminate use of these substances. *Pesticides and Pollution* is a more recent account of the problem.

DDT

Another type of 'chemical' control of pests is through the use of *systemic insecticides*—substances taken up by the plant and poisonous to the herbivore feeding on it, but not affecting any other animals. Analogous with this is the use of bacteria or viruses as insecticides—these, again, are highly specific and, although essentially 'biological', can be treated as chemical substances, stored and used as dusts, as and when convenient or necessary.

systemic insecticides

The use of sterile males is a different sort of biological control which has been successful with the screw-worm fly in the southern U.S.A. The theory is that the females which mate with the sterile males will lay eggs which

* An insecticide extracted from plants; the active principle is rotenone.

fail to develop. If sterile males form a large proportion of all males present, then a large proportion of the eggs must fail to develop. The practical problem is to raise sufficient numbers of males (which are then sterilized by exposure to radiation) to make any impact on the population; the effort required is worth while only when a major pest is involved and there is no easier safe method of control.

The future is likely to see a balance between chemical and biological control, with the use of each method where appropriate, and much greater care taken not to cause indiscriminate mortality of pests, predators, parasites and insects irrelevant to the problem. With a better knowledge of the life-histories of the organisms involved and improved understanding of the theories of population dynamics, it should be possible to use computers to work out the likely effects of different programmes and so to choose the best one.

A curious twist to the use of biological control is the recent development of a new method to control red spider mite on tomato plants in greenhouses. Red spider mite became a pest after the introduction of DDT, since it is very resistant to this substance and to all other pesticides. It can be regulated at a low level by a predator. To ensure that the predator will survive to exercise its regulation, the new technique is to introduce some red spider mites at the same time. Once the predator and prey populations are established, they will both keep going at a low level; this is low enough for the tomato plants to fruit freely and successfully. Previous efforts to use the predator sometimes failed because the predators died out before they had found enough prey to become established!

red spider mite

20.6.2 Human populations

Turn to *Population Dynamics*, p. 53: read section 7.8, then turn back to this text.

The rapid increase in human population since the seventeenth century has inevitably affected other species of organisms. The old agricultural populations have been replaced in certain parts of the world by communities founded on industry and technology (refer back to Unit 1 and to *The Roots of Present-day Science* for more details). Some of the effects of man on his environment can be classed under the general heading of 'pollution', and we shall refer to this again in Units 33 and 34. With increasing awareness of the problems and with improved technology, most pollution could now be reduced or prevented—but at a cost. The problems become economic and political. How can a politician balance the value of an amenity such as a clean river, where anglers can catch fish and people can swim or boat or simply enjoy a walk along the riverside path, against the thousands of pounds it may cost industry and the community to improve industrial and sewage effluents? Or the value of woods in city suburbs, where children and adults can 'enjoy nature', against the value of the site in terms of land for building houses or factories—or even motorways? These are the sort of problems where the conservationists must argue their case against industry and other cost-conscious sections of the community; there is usually no dispute about the scientific aspects of the ecological situations involved.

pollution

Other effects of man on the environment arise simply as a result of the increase in human numbers. These are problems of food and of living space, problems which can affect all species of animals. The second of these problems has rather been overlooked so far except in terms of the first (that is, that the increasing population will mean less land for food production); but it has been suggested that crowding may itself affect the

crowding

human population as it affects rats and voles when these animals are unnaturally crowded both in experiments and as the result of peak populations in the wild. In these rodents, stress symptoms appear; the adrenal glands are enlarged and the birth rate is reduced. Crashes in wild animal populations can also result from epidemic disease or from eating out of some important food resource. Human technology may be able to overcome these two last possibilities but, if there are hormonal effects of crowding, these may act as population-limiting devices.

20.6.3 Human food supplies

The food supply problem has been much discussed, though there remain two contrasting points of view. Many agriculturalists optimistically believe that, with the use of fertilizers, herbicides and pesticides, the world can produce enough food even for the enormous population predicted for the next century. On the other hand, many ecologists and others, knowing that at least half the population of the world is at present underfed, do not believe that it will be possible to produce enough to feed adequately the probable population of thirty years ahead. The estimates of these two groups of scientists differ widely; here we can only draw attention to the sort of problems which are relevant.

estimates of food supplies

If you turn to *Ecological Energetics*, p. 45, Figure 5.1, you can see how the proportion of the world population which is underfed has increased as the total population increased.

There are three main methods of improving this state of affairs: first, to stabilize or reduce the human population; secondly, to increase the efficiency of production and utilization of the present food sources; and, thirdly, to develop new food sources.

At present there is a high loss of food during transit from its source of production to its final utilization. Some of this loss of stored products occurs through pests—mice, beetles, flour moth and moulds—and could be avoided. Further research on the pests of stored foods should make the utilization of what is at present produced more efficient. Some food is lost for economic reasons such as the high cost of transport from areas of over-production to places where food is scarce; these political problems require political solutions. It seems on the face of it nonsense that producers should be burning food, or allowing it to rot, in one part of the world when people are actually starving or on the verge of starvation elsewhere.

The problems which we can reasonably discuss here are those of the efficiency with which different types of food can be produced in different environments and the likelihood of producing enough to fill the bellies of the future world population.

food production

Since energy is lost at each link of the food chain, the most efficient way for an omnivore like man to tap solar energy is to eat plants. Turn to p. 46 of *Ecological Energetics* and look at Figure 5.2. This shows the primary production in various types of ecosystem through the world. The highest figures for cultivated plants come from tropical agricultural crops such as sugar cane, which grow all the year round; for most agricultural crops the average annual production works out as between 3 and 10 g/m²/day. Turn to p. 37 of *Ecological Energetics* and look at Table 5—figures for annual production of various plants are given as metric tonnes/hectare. How is this related to the values of production in Figure 5.2?

1 tonne = 10^3 kg = 10^6 g; 1 hectare = 10^4 m²; 365 days/year so divide the values in Table 5 by 3.65 to make them comparable with the values in Figure 5.2. Notice that both sets of figures are for dry weight. What sort of conversion factor would you use to turn these into wet weights?

Most of the plants in Table 5 are not eaten by man. Usually only parts of crop plants are eaten by herbivores—the fruit, seeds, leaves or roots, but not all of them—so much of the primary production is not utilized. Plant proteins differ from animal proteins in proportions of amino acids; herbivorous animals have to consume large amounts of food simply to obtain certain essential amino acids. Consuming an animal diet is economical in terms of bulk of food to be consumed, although it is wasteful of solar energy. About 70 per cent of the present supply of protein for human food comes from vegetable sources and about 30 per cent from animal sources.

The majority of domesticated food animals are herbivores. But, as converters of solar energy into food available for man, there are marked differences between different herbivores. Figure 5.4 of *Ecological Energetics* illustrates the contrast between cattle and rabbits; the rabbits produce the same weight of meat from a given amount of hay as do beef cattle, but they do so in 30 days instead of 120, so their production is more efficient per unit time. Intensive livestock rearing is the most efficient way of producing those animal proteins which are traditional foods. The chickens and calves are harvested when young and still growing fast; they are fed on processed diets which incorporate parts of plants (and animals) normally discarded as inedible. Sometimes unfortunately, substances are added to their diet that may be dangerous to people, such as, for instance, antibiotics and hormones.

Ideally, protein should form about 10 per cent of total food intake, measured in terms of energy. The really big difference between the diets of well-fed and under-fed peoples of the world is, in fact, in the amount of protein eaten. An adequate diet should contain about 44 g/day: in North America, the present average consumption is about 64 g/day whereas in underfed areas it is about 9 g/day.

Apart from the traditional domesticated animals, there are two main sources of animal protein—wild mammals and fishes.

Wild mammals are principally of interest in the tropics and in the polar regions (seals, whales and polar bears). There is a strong case for harvesting wild game in parts of Africa, instead of introducing domesticated cattle and goats. The wild game are adapted to the natural ecosystem and the many species of antelope together with zebra, rhino, elephant and hippo presumably rely on slightly different plants and therefore can all flourish together. Introduced cattle eat only a limited range of plants and are not adapted to the local climate nor capable of withstanding the local diseases.

Sea fisheries depend on harvesting natural populations of fish. Some of the problems involved are discussed in this Unit's TV programme. Optimum exploitation, maintaining a good yield without damage to the breeding stock, depends on careful manipulation of the fishing effort so that the numbers and sizes of fish caught are regulated. The scientific principles basic to this rational exploitation are well understood, but their application depends on international co-operation—so far this has been achieved only in very few cases. Managing wild populations of whales, seals and polar bears depends on exactly similar principles to those basic to the fishing industry. The present disastrous state of whaling in the Antarctic is a sad example of the effects of over-fishing, carried out in the face of repeated warnings by marine biologists, and in spite of the fate of whales in northern

As you read in Unit 14, water comprises at least 60 per cent of most living organisms. For realistic values, you should probably multiply the figures by at least 3 to obtain the primary production in wet weights.

domesticated food animals

wild mammals

sea fisheries

waters. Many of these marine sources of first class protein are carnivores—a new threat to them is the pollution of the sea by substances which pass along food chains and accumulate in top carnivores. Insecticides such as DDT, fungicides containing mercury, PCBs (poly-chlorinated-biphenyls) used in industry, and other substances can reach the sea through industrial and sewage effluents or run-off from the land; their accumulation in fishes could affect disastrously the potential food supply for the rising world population.

In 1962, there were 1.3 acres of arable land per person, and it is estimated by FAO* that the figure will be 0.7 acres per person by 2 000 A.D. This implies that merely to maintain the present levels of nutrition by agriculture alone would involve doubling the productivity of the arable land—a very unlikely prospect. It is possible that the production from the sea could be doubled and production of terrestrial animal protein might be increased by rather more than 50 per cent; there are possibilities of increasing freshwater fish production by more than 10 times. Between them, these actions would just about double the amount of animal protein available in 2 000 A.D.

There are other possible sources of food: proteins can be extracted from leaves to provide a nutritious diet lacking only the essential amino acid lysine; a bacterium converts petroleum into protein which can then be harvested; biochemists could produce synthetic foods. All these sources can be exploited only through manufacturing processes which use energy; the amount of energy necessary to produce the edible protein may be so great that the source is totally uneconomic. Indeed, since the manufacture of synthetic fertilizers requires expenditure of energy, the use of increased quantities of fertilizer means faster consumption of the world's reserves of fossil fuels, as also does the increased use in agriculture of insecticides, herbicides and other synthetic substances. The machines that apply these substances to the land and the mechanical harvesters that collect and process the crops also use considerable quantities of fossil fuel. Feeding the world population uses up a great deal of energy—the reserves of fossil fuels are being depleted rapidly.

new sources of food

energy requirements of food production

Nuclear energy, or some process for using the solar energy at present wasted, will be essential if a large human population is to survive in the future. A new source of protein obtained by a process based on one of these types of energy could make it feasible to feed three or more times the present population of the world. The limit to population increase might then be set by density-dependent physiological or psychological reactions. We can observe these operating for other species of animals, but at present we know very little about such reactions in human populations.

Now you can attempt SAQs 15 to 19. These relate to the whole Unit.

If you wish, you can read *Ecological Energetics*, chapter 5, and *Population Dynamics*, the rest of chapter 7, as black-page Appendices to section 20.6.

* The Food and Agriculture Organization of the United Nations.

20.7 Summary

All individual organisms belong to assemblages of individuals called communities; these usually include individuals of many different species. Individuals and species are not randomly distributed. The composition of any given community can be understood in terms of food webs and of the 'flow' of energy and of essential elements through it; these can be represented as diagrams and also as several different types of ecological pyramid.

Each species in a community occupies a 'niche', defined by its food relations and life-history. The geographical distribution of species depends on where they evolved, how individuals can be dispersed, how tolerant individuals are of various environmental conditions summed up as climatic and edaphic factors, and how successfully individuals can find food resources and can survive in the 'struggle for existence' (in the face of predation, parasitism and competition).

Studying population numbers involves careful sampling techniques. It is important to measure the fecundity (or numbers of young produced) and the mortality factors operating at different ages or stages. Survivorship curves and curves of population change with time show considerable differences between species. Analysis of mortalities using k -values reveals which are the 'key factors', mainly responsible for changes in numbers, and which are the 'regulating factors' that tend to stabilize the population by altering the numbers in the direction of the average values. This type of analysis is described for an insect (winter moth) in the text and for a bird (tawny owl) in Appendix 1.

Natural communities change with time towards a fairly stable 'climax'. Interference with communities may cause considerable changes, not fully predictable at our present stage of knowledge. The impact of the virus disease myxomatosis on rabbit populations in Australia and in the British Isles, and the consequent changes are examples of effects on communities resulting from human actions.

Human civilization has considerable effects on other organisms; the emergence of weeds and pests and some methods of pest control are studied as special examples. Finally, some of the problems of the expansion of the world human population are discussed with special reference to food and energy requirements related to energy flow in different types of community.

Tawny Owls

The information in this Appendix is taken from a study of tawny owls on the Wytham Estate, near Oxford. For the full account, see: H. N. Southern (1970) 'The natural control of a population of tawny owls (*Strix aluco*)' *Journal of Zoology*, Vol. 162, pp. 197–285.

1.0 The life history of the tawny owl

The tawny is the most common owl species in Great Britain, where it is widely distributed in woodlands, open ground and cities, wherever there are some large trees. It roosts in trees by day and becomes active at dusk; its method of hunting is to perch on a low bough of a tree and then drop on to its prey, which it probably detects by the sounds made. This species of owl nests in holes in trees—thus large trees are absolutely essential for its way of life.

Tawny owls are highly territorial (see 20.4). They probably spend their whole adult lives in one area. They have characteristic calls so that it is possible to locate the birds and to recognize what they are doing at certain times and seasons.

A typical year in the life of a pair of tawny owls is as follows.

August and September The birds moult (i.e. they lose their feathers and grow a new set); at this time they are silent and inconspicuous.

moult

October and November Each pair of birds asserts its territory. Each owl spends 15 to 20 minutes at dusk hooting (hōoo-hu-hū, -hū, -hū, -hōoo) from a prominent tree. Later the owls hunt for food. If an owl encounters an owl other than its mate, it challenges noisily by 'caterwauling'. The limits of the territories are established by noisy encounters between the residents. Each resident owl is reluctant to leave its own territory.

establishment of territory

December to February The owls begin to indulge in courtship behaviour. They choose a nest site, a hole in a tree; they roost together, often near the nest site. The male brings food to the female who calls softly (oo-wip) to attract him.

March to May This is the breeding season. The female lays up to four eggs and begins to incubate (to sit on them) after she has laid two. She stays on the nest, leaving it only when the male brings her food. When the eggs hatch, the female stays with them until they are halfway to being 'fledged' (able to fly); she tears up food brought by the male and distributes it to the owlets. When they are half grown, she starts to help the male to collect food for them.

breeding

June to August The owlets become fully fledged and leave the nest. They explore their parents' territory, but still rely entirely on their parents for food. Owlets call (ti-swerp or ti-swoop) at dusk and through the night; this shows their parents where to find them with food.

rearing young

August and September The owlets disperse and must start to fend for themselves. Some pair, find territories and may breed in the following year. The adults start to moult and the annual cycle is then repeated.

Question 1 Using the information given above, suggest possible methods and times for carrying out censuses of the tawny owl population in a given area.

Read Answer 1 (p. 62).

1.1 Territories of tawny owls on the Wytham Estate, Nr. Oxford

Southern started his study in 1947, after a winter of prolonged frost and snow when many adult tawny owls died probably from starvation. In that autumn, there were only 17 pairs of owls occupying territories on the estate. The numbers increased gradually; in the five years from 1955 to 1959 (the end of the study) there were 30, 32, 32, 31 and 32 territories, suggesting that 32 is the upper limit to the viable number on this estate. The study therefore covers a period when the density of pairs of owls was increasing towards and then settling down at this maximum value. We shall refer to this later.

The estate, of total area $525 \times 10^4 \text{ m}^2$, includes dense woodland, open woodland and parkland. In the later years, the mean area of each territory was $16 \times 10^4 \text{ m}^2$, but territories in open parkland were always larger than those in woodland. The boundaries of some territories remained remarkably constant from year to year. The same pair of owls was known to occupy certain territories for seven years or longer; on average, each pair of owls occupied a territory for five years. In the first year or two, the pair often failed to rear young, but usually they bred successfully in the later years of their occupation of the territory.

Question 2 Suggest an explanation for the observations in the last sentence.

Read Answer 2 (p. 62).

Question 3 In the light of these observations, suggest a possible survival value of the owls' territorial habit.

Read Answer 3 (p. 62).

1.2 The food of tawny owls at Wytham

Owls are carnivores, but there is seasonal variation in their diet.

Between December and February, about 80 per cent of their diet consists of small mammals, principally wood mice and bank voles. From May to August, moles, young rabbits and invertebrate animals such as earthworms and beetles become the principal items in the diet. Over the whole year, mice and voles comprise about 50 per cent of the vertebrate animals of the diet; these animals can be caught alive in traps, marked and released so that they can be counted. Here are some facts about them:

(a) The wood mouse *Apodemus* is strictly nocturnal in habit. By day it lives in burrows; it comes out at night and forages over the open woodland floor eating mainly seeds but, especially in spring, also some insects. It

owl territories

wood mouse

breeds between April and October. Its numbers are least in early spring and greatest usually in the autumn.

(b) The bank vole *Clethrionomys* may be active at all times of day and night, but each individual probably has a rhythm of activity and rest. It feeds on live and dead herbaceous material, and usually moves about under shrubs and avoids open spaces. It breeds at the same time as the wood mouse, but may continue longer into the winter. The numbers are usually low in May and June and reach a peak in autumn or winter.

bank vole

Of the other animals in the diet: moles eat insects and earthworms; earthworms eat dead leaves; the beetles eaten by owls include cockchafer, which are herbivorous, and ground beetles, which are carnivorous, eating other insects.

Question 4 From the information given above, construct a food web for tawny owls at Wytham.

See Answer 4 (p. 63).

Figure 11 gives the results of censuses of wood mice and bank voles carried out at intervals of six months. The scale is arithmetic.

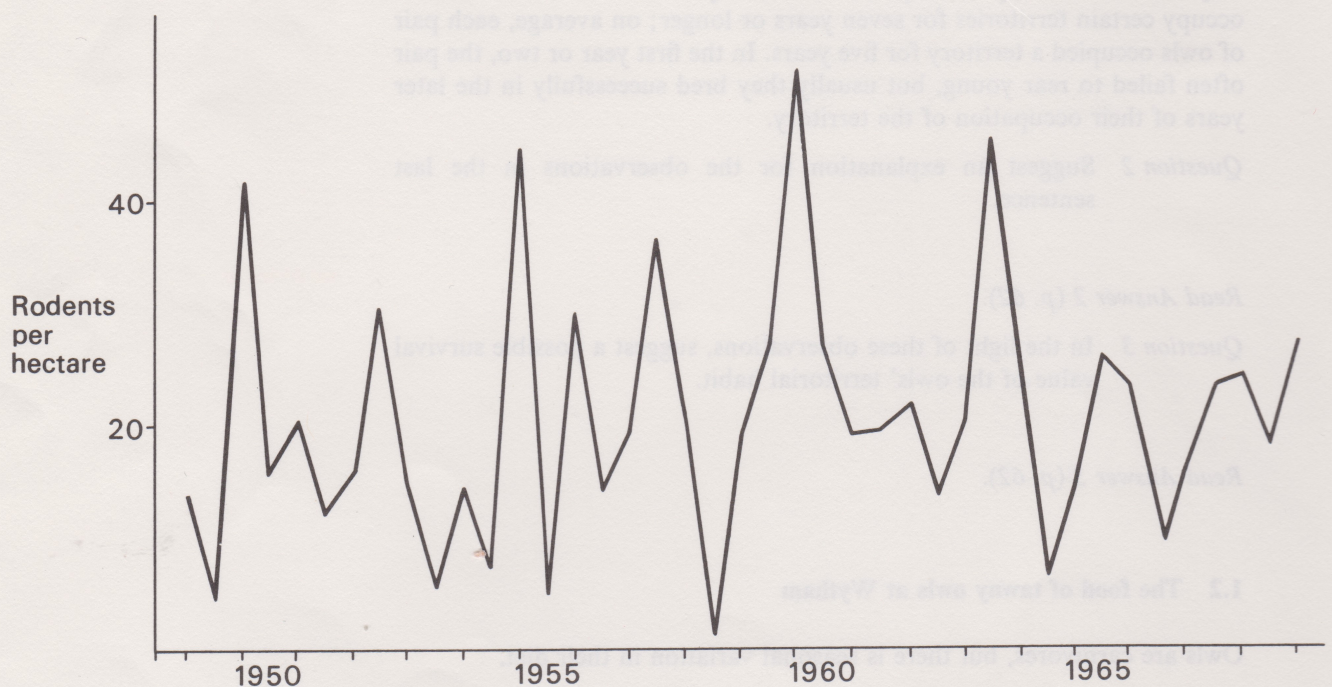


Figure 11 The numbers of small rodents (wood mice and bank voles) estimated at six-monthly intervals in Wytham Wood.

Question 5 How are the highest and lowest numbers of these small rodents related to each other?

Question 6 Do the fluctuations appear to follow a regular cycle?

Question 7 What, approximately, is the average number of small rodents per hectare ($= 10^4 \text{ m}^2$)?

Read Answers 5, 6 and 7 (p. 63).

The detailed figures show that the greater part of the fluctuation in numbers is of numbers of bank voles. Wood mice seldom exceeded 10 ha^{-1} ; the totals for the two species fluctuated about an average of 20 ha^{-1} ; on three occasions, the numbers of bank voles approached 40 ha^{-1} .

Question 8 Suggest a hypothesis connecting these observations on bank voles and wood mice with the numbers of tawny owls.

Read Answer 8 (p. 63).

1.3 Life tables for tawny owls at Wytham

If tawny owls are provided with suitable boxes, they will nest in them, so that it is possible to observe whether a given pair lays eggs or not, whether the eggs all hatch and whether all the chicks are fledged. Chicks can be marked with rings and some information about survival of fledged chicks can be obtained from analysis of when and where these rings are recovered.

Here is the life table for tawny owls at Wytham:

Average number of eggs laid: 62

Age in years	Average number surviving at the end of the year	
0-1	19	
1-2	9	
2-3	7	survivorship
3-4	6	
4-5	5	

Question 9 Construct a survivorship curve for tawny owls at Wytham.

Here is part of the detailed information collected.

	Data for 1952
Number of pairs of owls present on the estate	24
Number of pairs attempting to breed	17
Average number of eggs laid per nest	2.5
Eggs lost before hatching (as percentage of total)	62
Chicks lost between hatching and fledging (percentage of total)	6
Average annual mortality of adult owls (percentage of total)	18.5
Number of pairs of owls present in the following year (1953)	24

Question 10 Use the figures given above to construct a survivorship curve for the eggs and young of 1952.

Look at Answers 9 and 10 (p. 64).

1.4 Key factor analysis for tawny owls at Wytham

The average maximum clutch size was 3 eggs per pair, so the maximum number of young that are likely to be produced each year can be derived by multiplying the number of pairs in the area by 3. This maximum was never achieved during the period of observation.

The following mortality factors were quantified: (Refer back to 20.4 for definition of k -values).

- k_1 the number of eggs 'lost' through failure of the adults to breed; (the k -value is the log of the number of pairs failing to breed multiplied by 3).
- k_2 the number of eggs 'lost' through failure of those pairs that nested to lay the maximum clutch of eggs—the average clutch size was 2.5 eggs per breeding pair.
- k_3 the number of eggs lost before hatching. Most of this loss was the result of desertion of the nest by the female.
- k_4 the number of chicks lost before fledging. Most of these died either before their eyes opened or while the feathers were growing.
- k_5 the number of young dying between leaving the nest and acquiring territories of their own in the following spring.

k -values

Figure 12 shows the k -values derived from the data for 1949 to 1959 inclusive.

Examine this graph, then answer the following questions.

Question 11 Which is the 'key' factor?

Question 12 Do any other k -values vary in the same way as the key factor?

Question 13 Do any k -values appear to vary in the opposite way from the key factors? (that is, are any of the k -factors compensating, density dependent factors?)

Read Answers 11, 12 and 13 (pp. 64–5).

The key factor analysis has shown which mortalities are responsible for the fluctuations of the population numbers and which mortality acts in a way that should stabilize the numbers. Can we relate these mortalities to any environmental factors that vary at Wytham?

Question 14 Consider what you have already read about tawny owls and then suggest environmental factors that are worth detailed evaluation.

Read Answer 14 (p. 65).

1.5 Mortality and food supply (in the form of bank voles and wood mice)

Probably adult owls died of starvation during the long snowy winter of 1946–7, just before the beginning of these observations, but Southern found no evidence of *adult* mortality varying with food supply between

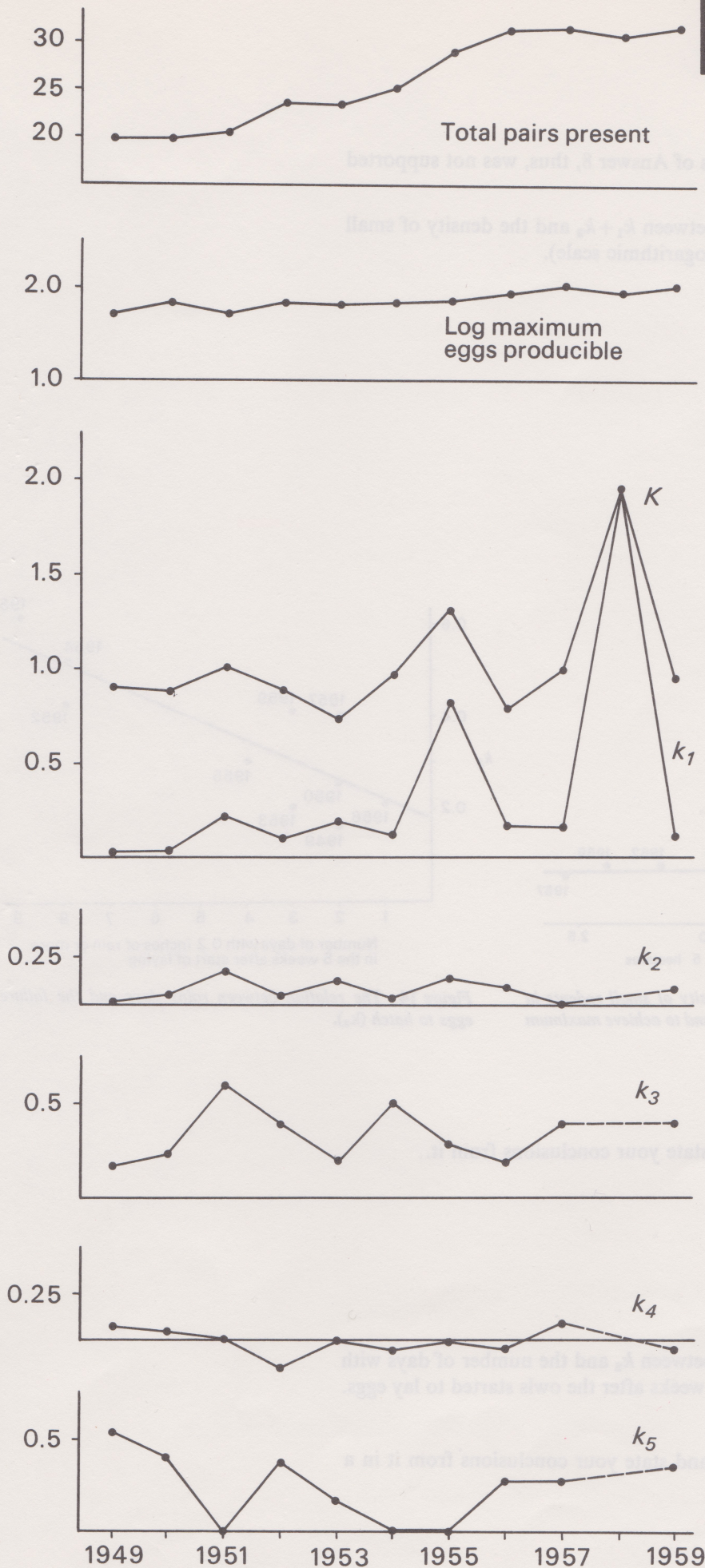


Figure 12 K and k-values for tawny owls in Wytham Wood.

1947 and 1959. The first hypothesis of Answer 8, thus, was not supported by the results of this investigation.

Figure 13 shows the relationship between $k_1 + k_2$ and the density of small rodents in spring (expressed on a logarithmic scale).

Examine Figure 13.

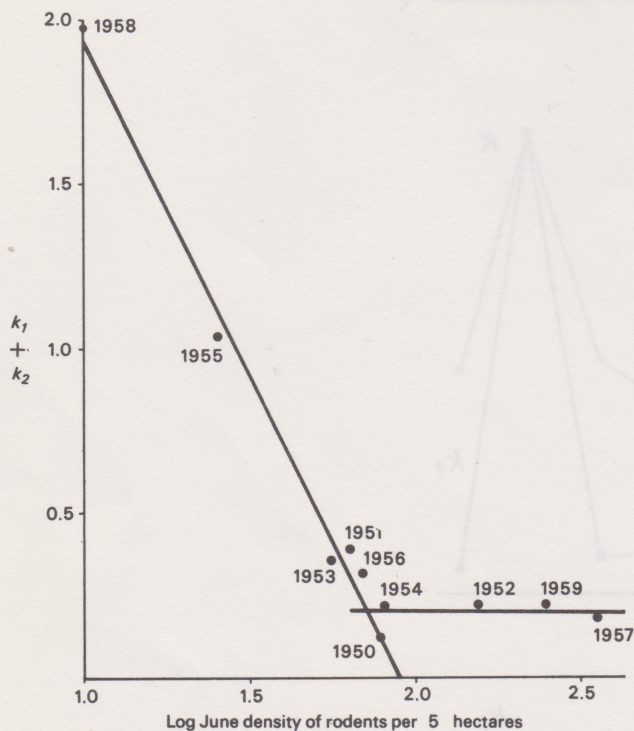


Figure 13 The relation between the density of small rodents in June and 'losses' through failure to breed and to achieve maximum clutch size ($k_1 + k_2$).

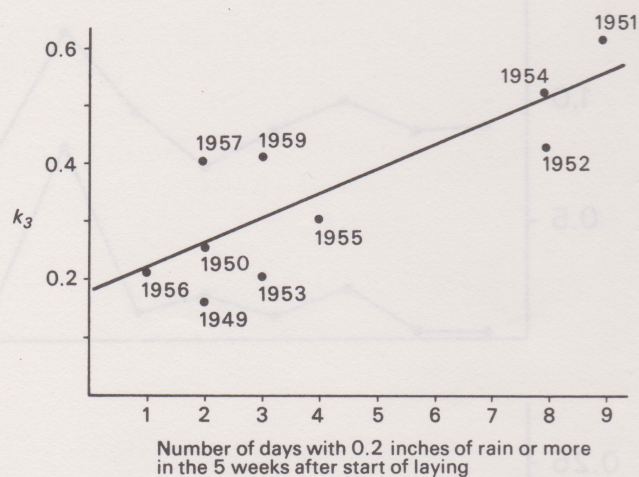


Figure 14 The relation between rainy days and the failure of eggs to hatch (k_3).

Question 15 In a few sentences, state your conclusions from it.

Read Answer 15 (p. 65).

1.6 Mortality and weather

Figure 14 shows the relationship between k_3 and the number of days with 0.2 inches or more of rain in the 5 weeks after the owls started to lay eggs.

Question 16 Examine Figure 14 and state your conclusions from it in a few short sentences.

Read Answer 16 (p. 66).

1.7 Mortality and the density of the population

Figure 15 shows k_5 plotted against the number of young fledged in that year (on a log scale). The negative values for k_5 indicate that owls migrated into Wytham from other areas; this happened in years when an insufficient number of owlets survived on the estate to replace the adults that died.

- Question 17 Does Figure 15 indicate that k_5 acts as a density-dependent factor?
- Question 18 If you answered 'yes' to Question 17—Does k_5 act as a compensatory 'regulating' factor?

Read Answers 17 and 18 (p. 66).

Figure 16 shows the relation between the average number of young fledged per territory and the number of adult owls (expressed as the number of territories on the estate).

- Question 19 Examine Figure 16 and state your conclusions from it in a few short sentences.

Read Answer 19 (p. 66).

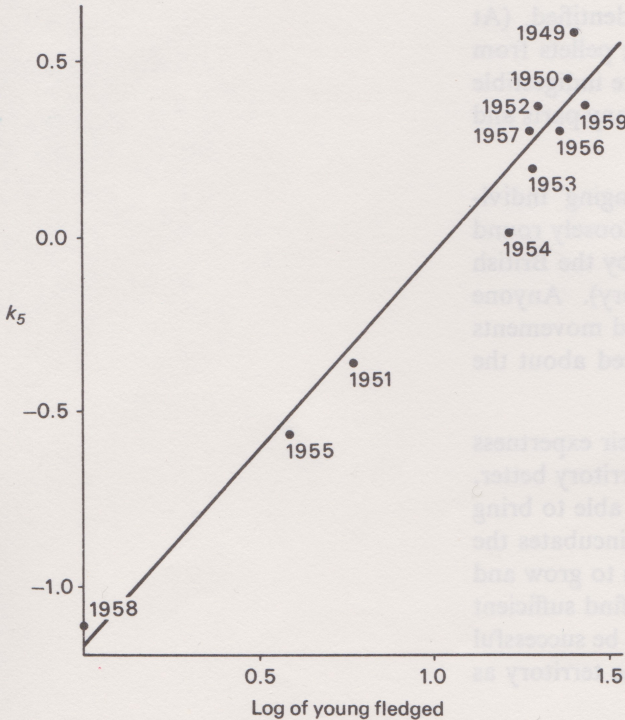


Figure 15 The relation between the number of young fledged and the overwinter disappearance of yearling owls (k_5).

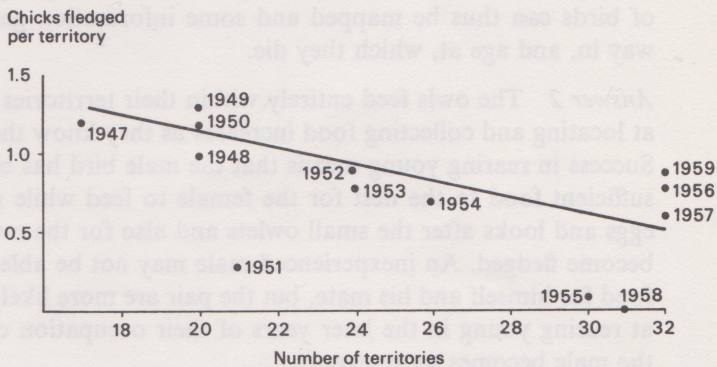


Figure 16 The relation between the number of territories held and the number of young fledged.

Finally: write a short summary listing the factors that control the population of tawny owls at Wytham. Compare your summary with that in section 1.9, p. 66.

1.8 Answers to the questions

Answer 1 Each pair of adult owls stays in its own territory, so it is possible to map the territories over a period of weeks and deduce the number of adult birds. Although the owls are nocturnal and fly silently, their calls allow observers to locate and count them.

October to November Hooting at dusk (Southern organized a large band of helpers on one evening each year to locate as many owls as possible during the 20 minutes after dusk when the owls called). The 'caterwauling' at the edges of territories allows them to be mapped. Owls roused from their roosts during the day refused to cross territorial boundaries and would 'bounce back', to use Southern's graphic description, marking the edges precisely.

December to March The females' calls during courtship, mating and nesting allow the pairs to be located and counted.

June to early August The calls of the young allow them to be located and counted.

Owls nest in holes in trees, but will use a suitable nesting box, which can be fitted with a mirror. They cannot 'see' red light and can be observed at night using a red torch. It is possible to locate many of the nests and to count the numbers of eggs laid and the numbers of young hatched and fledged. Food brought to the nest can be observed and identified. (At other times of year, the food can be deduced by collecting pellets from under the trees in which the owls roost when they regurgitate indigestible parts of their food—small mammals can be identified from bony parts and some insects from their hard wings or heads.)

Juvenile birds leave their parents' territory in August so 'ringing' individuals can be a census aid—a numbered metal band is fixed loosely round one leg; the numbers are recorded in a central register run by the British Trust for Ornithology, British Museum (Natural History). Anyone finding a bird with a numbered ring informs this registry and movements of birds can thus be mapped and some information gathered about the way in, and age at, which they die.

Answer 2 The owls feed entirely within their territories; their expertness at locating and collecting food increases as they know the territory better. Success in rearing young means that the male bird has been able to bring sufficient food to the nest for the female to feed while she incubates the eggs and looks after the small owlets and also for the owlets to grow and become fledged. An inexperienced male may not be able to find sufficient food for himself and his mate, but the pair are more likely to be successful at rearing young in the later years of their occupation of the territory as the male becomes more expert.

Answer 3 The habit spaces out the owls, giving each pair an area in which they can seek food without interference or competition from other owls. Since the population survives, the areas of the territories must be adequate as sources of food for a pair of birds and their offspring in

average years. The information from Wytham suggests that smaller territories suffice in woodland compared with parkland—on this estate an average of 16 ha seems to be the minimum area that is adequate for survival.

Answer 4

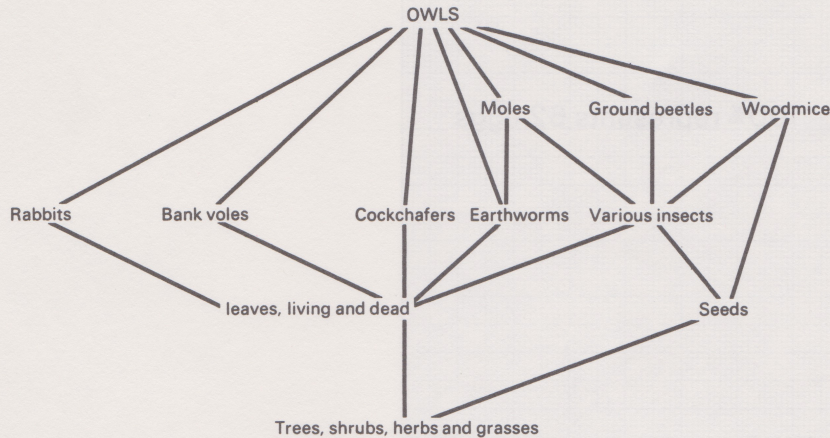


Figure 17 Food web for tawny owls in Wytham Wood.

Answer 5 The lowest figure recorded is that for winter 1958—approximately 1 small rodent ha^{-1} . The highest figure is that for spring 1959—approximately 50 ha^{-1} . So the highest value is about 50 times the lowest.

Answer 6 No, there is no regularity.

Answer 7 Approximately 20 ha^{-1} .

Answer 8 Bank voles and woodmice together form a substantial part of the diet of tawny owls, so fluctuations in numbers of small rodents may lead to fluctuations in numbers of tawny owls. About 80 per cent of the diet in winter consists of the two rodent species, whereas the diet in summer includes more other mammals and invertebrates than bank voles and wood mice. Here are two possible hypotheses.

- 1 When the rodent population is low in autumn and winter, the survival of tawny owls through the winter will be low—there will be fewer adults in the following spring.
- 2 When the rodent population is low in the winter and early spring, the breeding success of the tawny owls will be below average—since the males will find it difficult to bring enough food for the females to lay and incubate eggs in March and April. Females without sufficient winter food also may not be able to produce as many eggs as those with plenty of winter food.

Answer 9 See Figure 18. Starting with 62 eggs, the numbers of survivors are plotted as quoted in the life table.

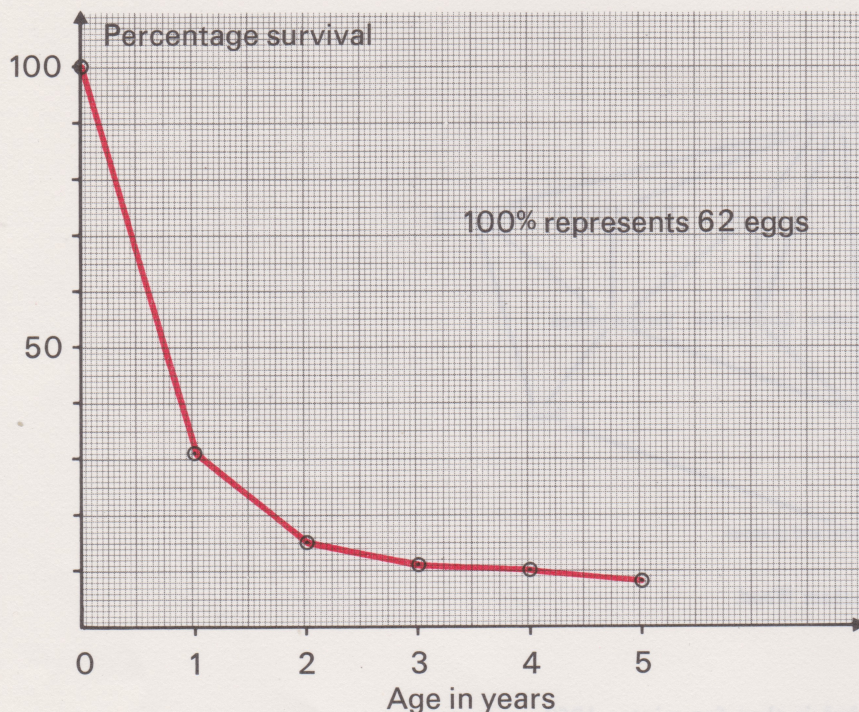


Figure 18 Average survivorship curve for tawny owls.

Answer 10 The information needs manipulation before the curve can be plotted. The figures needed are as follows:

- Total number of eggs laid (in March).
- Total number of eggs that hatch into chicks (in April).
- Total number of chicks that become fledged (in June).
- Total number of young owls that survive to form pairs in the following March.

To obtain (a) multiply the number of pairs attempting to breed by the average numbers of eggs laid per nest: $17 \times 2.5 = 42.5$.

To obtain (b) multiply the number of eggs laid by the percentage survival of eggs (100 – 62 per cent): $42.5 \times 38 \times 10^{-2} = 16$.

To obtain (c) multiply the number of chicks hatched by the percentage survival of chicks (100 – 6 per cent): $16 \times 94 \times 10^{-2} = 15$.

To obtain (d) note that the number of pairs of owls in 1953 was the same as that in 1952 (24 pairs). But 18.5 per cent of the adult owls died during the winter. Thus the number of owlets that survived to form pairs in 1953 must equal the number of adult owls that died during the winter: $24 \times 18.5 \times 10^{-2} \times 2 = 9$.

These figures are plotted to give the curve in Figure 19.

Answer 11 k_1 is the key factor. In 1958 it accounted for the total loss of recruits to the population.

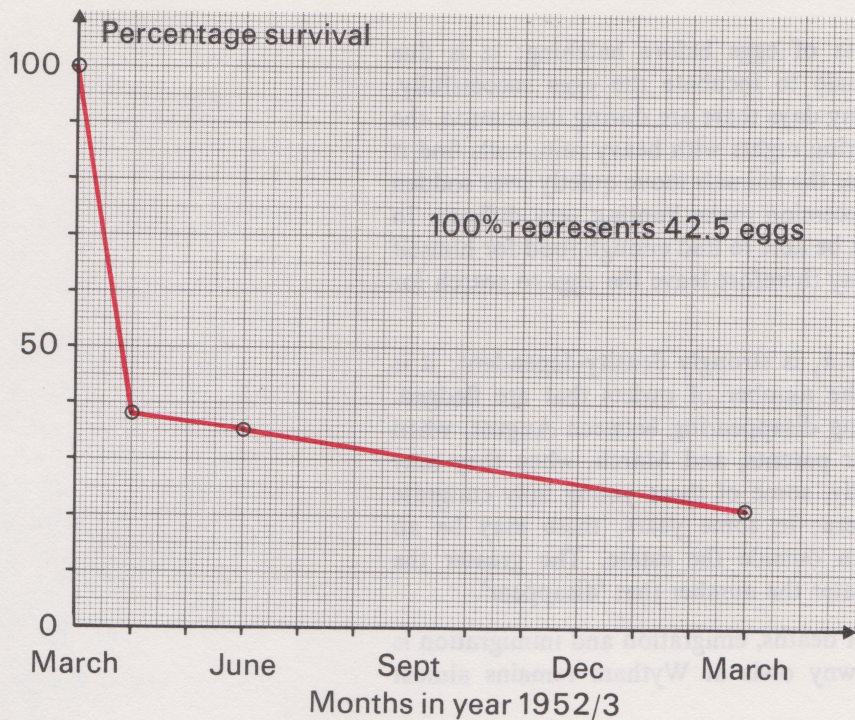


Figure 19 Survivorship curve for the eggs and the young of 1952.

Answer 12 k_2 varies in the same way as k_1 , but is not so large. k_3 varies in a similar way to k_1 in some years (e.g. 1949–52) but in a quite different way in other years (e.g. 1953–55).

Answer 13 k_5 appears to vary in the opposite way from k_1 so that it tends to restore the level of the population towards the average value from extreme high or low values.

Answer 14 (a) The English climate is very variable so that it might be worth evaluating the relation between k -values and temperature and rainfall.

(b) Variations in numbers of small rodents might lead to fluctuations in survival or in breeding success of owls (see answer 8).

(c) The number of pairs of owls on the estate rose steadily from 1947 to 1955 (see section 1.2, p. 55). k_1 is lower in the early years than it is in 1955 or 1958; it might be worth investigating the relation between k values and density of adult owls.

Answer 15 $k_1 + k_2$ represents the 'losses' resulting from failure of some pairs of owls to breed and failure of those that bred to lay the maximum number of eggs. These losses are very high when the density of small rodents was very low in spring (in years 1955 and 1958); there is an inverse correlation between losses and the density of rodents for rodent populations below about 20 rodents ha^{-1} . Above this value, the mortality is at a constant low value; the breeding success of the owls is not increased even when the rodent density is 70 ha^{-1} . We may conclude that the breeding success of tawny owls at Wytham is dependent on the density of the rodents that are their principal food in early spring, if this density is less than about 20 animals ha^{-1} . Above this density, losses through failure to breed are comparatively low and independent of the numbers of rodents.

Answer 16 k_3 represents the loss of eggs before hatching; it is due principally to failure of the female to incubate the eggs successfully. Figure 14 shows that the more rainy days there are during incubation, the greater are the losses of eggs. During nights with heavy rain, owls find it difficult to detect their prey because the animals move quietly over sodden leaves; several rainy nights in succession make hunting very difficult. In such conditions, the male may not be able to find enough food for himself and the incubating female; she may therefore leave the eggs to search for food for herself.

Answer 17 Figure 15 shows that k_5 is strongly density-dependent; it is almost exactly proportional to the number of owlets that are fledged. k_5 represents the number of young disappearing between August, when they become independent of their parents, and March, when they may start to breed themselves. Actually, some of these young may emigrate and establish themselves elsewhere; in some years, there may be an immigration of young owls from outside the estate. The greater the number of fledged owlets, the greater the number that 'disappear'.

Answer 18 Yes. The net result of deaths, emigration and immigration is that the population of adult tawny owls at Wytham remains almost constant.

Answer 19 As the number of territories increased, the average number of chicks fledged for each pair of owls decreased from about 1.2 (in 1947) to about 0.5 (1957). Values for three years (1951, 1955 and 1958) lie well below the line drawn on the graph but show a similar trend. If you check these years in Figure 11, you will find that the numbers of rodents were low in the winters. Figure 16 shows that the more adults there were present, the greater the failure in breeding performance and the fewer the number of fledged young per territory.

1.9 Summary

To quote Southern's own words:

- 1 The success of the tawny owls in Wytham in laying eggs, hatching them and in fledging young is determined by the general level of the abundance of mice and voles. This relationship finds its saturation point when the density of prey reaches 100/12 acres (approximately 20ha^{-1} , *Ed.*). Beyond this, breeding success is no further advanced.
- 2 The distribution of losses (i.e. failure to achieve the maximum possible) between stages of the breeding cycle shows that refusal to breed at all and failure to reach the maximum clutch size follow the total of losses closely (i.e. they represent 'key factors' in this terminology). The failure to hatch eggs, either by deserting them and/or allowing them to become chilled, also represents a heavy loss, though, if it also follows the trend of total losses, this is obscured by the sporadic, distracting influence of rainy weather. Failure to fledge the young that have been hatched, although often hailed as a notable adaptation of predators to a variable food supply, is shown to be, relatively, of little account.
- 3 The magnitude of these losses, depending upon the numbers of prey, is usually not sufficient to scale down the number of young produced to a point where they will replace, more or less exactly, the adults that die during a year. The adjustment takes place after fledging and during the ensuing winter, when the recently fledged young fail to secure territories within Wytham and either die there from starvation or emigrate to other areas. Nevertheless, in a few years when prey was unusually scarce, so few young were produced, that movement across the boundary of the estate was reversed.

Self-Assessment Questions

Section 20.1

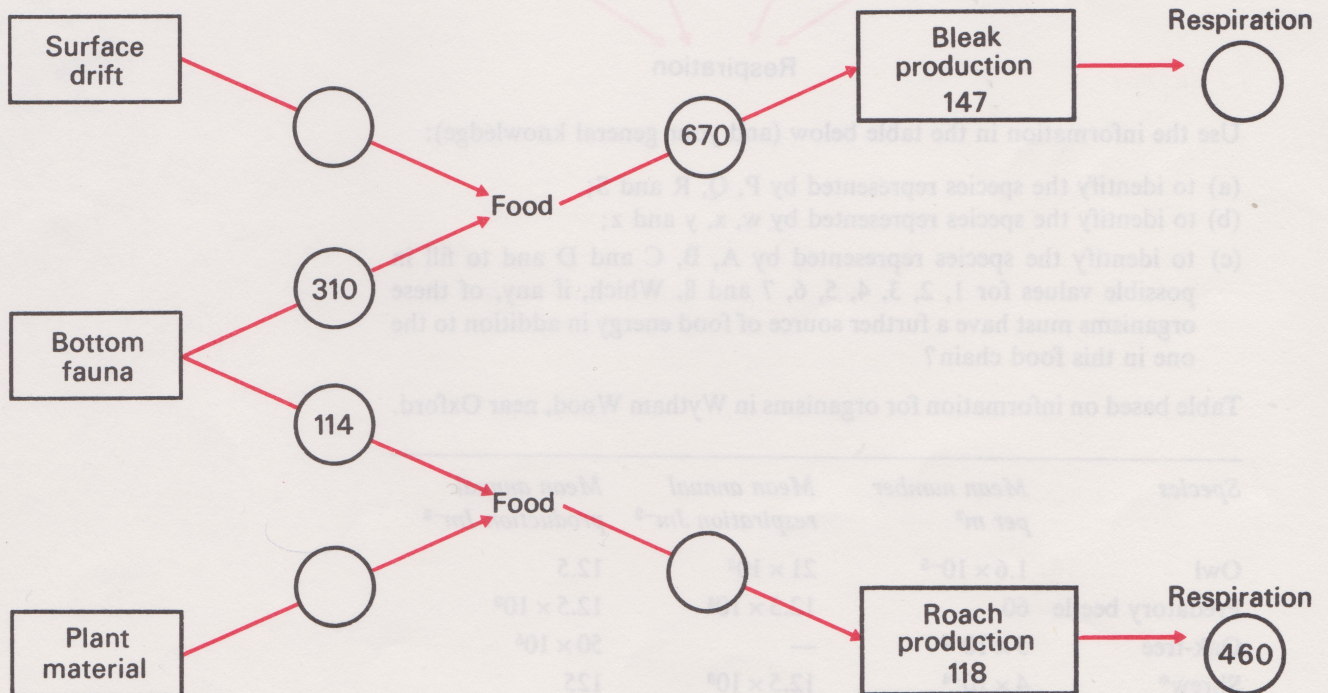
Question 1 (Objective 1)

Mark the following statements as either TRUE or FALSE.

- (a) A community consists of many organisms all of the same species.
- (b) Plants are primary producers; they 'fix' some of the energy of sunlight by the process of photosynthesis.
- (c) Consumers and decomposers are heterotrophes.
- (d) Carnivores are autotrophes.
- (e) Energy flows through a community and then is recycled and flows through again.
- (f) Most natural communities include plants, animals and micro-organisms.
- (g) In any community, the number and biomass of carnivores is usually greater than the number and biomass of herbivores.
- (h) Parasites are usually smaller and more numerous than their hosts.

Question 2 (Objective 4)

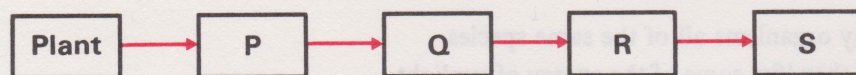
In the following diagram, the figures are given in 10^3 Jm^{-2} per annum. Assuming that there are no other connections in the food web, fill in the values of the blanks.



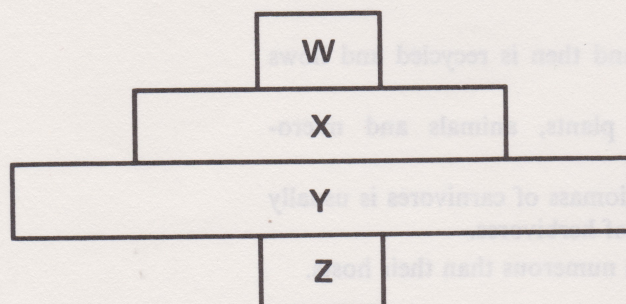
Question 3 (Objective 2)

There are three series of boxes below.

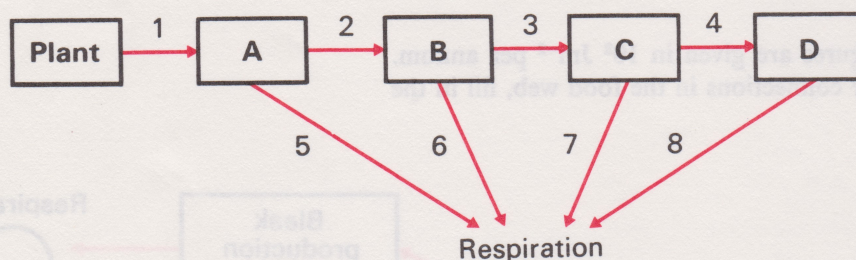
(a) These boxes represent a food chain.



(b) These boxes represent a pyramid of numbers.



(c) These boxes represent an energy flow diagram.



Use the information in the table below (and your general knowledge):

- to identify the species represented by P, Q, R and S;
- to identify the species represented by w, x, y and z;
- to identify the species represented by A, B, C and D and to fill in possible values for 1, 2, 3, 4, 5, 6, 7 and 8. Which, if any, of these organisms must have a further source of food energy in addition to the one in this food chain?

Table based on information for organisms in Wytham Wood, near Oxford.

Species	Mean number per m ²	Mean annual respiration Jm ⁻²	Mean annual production Jm ⁻²
Owl	1.6×10^{-5}	21×10^3	12.5
Predatory beetle	60	12.5×10^4	12.5×10^3
Oak-tree	3×10^{-3}	—	50×10^5
Shrew*	4×10^{-4}	12.5×10^3	125
Winter moth caterpillars	10^2	30×10^4	35×10^3

* A relative of the hedgehog; it feeds on insects.

Question 4 (Objective 3)

The matrix below contains 9 statements about metabolic capacities of groups of organisms. Choose from this matrix the statements which are true for each of the organisms in the following list; write the number of each of these statements after the organism. You may use each statement once, several times or not at all.

List of Organisms

Oak-tree	Caterpillar
Owl	Man
Grass	Decomposing bacteria

1 convert amino acids into mineral salts	2 convert proteins into ammonia	3 use the energy of sunlight
4 convert nitrogen into nitrates	5 convert carbon dioxide into sugars	6 use the energy in sugars
7 convert sugars into carbon dioxide	8 convert mineral salts into amino acids	9 convert sugars into amino acids

Section 20.2

Question 5 (Objective 1)

Mark the following statements as either TRUE or FALSE.

- (a) Predators are nearly always smaller than their prey.
- (b) Many herbivores restrict their feeding to a small number of plant species.
- (c) Detritus feeders consume only organisms smaller than themselves.
- (d) The same animal occupies the same niche all over the world in all climates.
- (e) The distribution of plants over the world is greatly affected by climate.
- (f) Within climatic belts, the distribution of plants is not affected at all by the type of soil and other edaphic factors.

Question 6 (Objectives 5 and 11)

Salmonid fishes can live in water with ice on it, but not at temperatures above 30° C.

Cyprinid fishes can live in water with ice on it and at temperatures up to 42° C.

Cichlid fishes can live only between the temperature limits of 20° to 35° C.

Given that the three statements above are true, which of the groups of fishes would you expect to find in the following waters:

- (a) Lake Victoria in East Africa;
- (b) Great Bear Lake in northern Canada;
- (c) Lake Balaton in Hungary;
- (d) fish ponds in Malaya and Nigeria;
- (e) fish ponds in Sweden and Ireland;
- (f) fish ponds in Israel and Poland.

Question 7 (Objectives 11 and 13)

Avocado pear trees do not grow wild in the British Isles. Possible reasons for this are:

- (a) that the climate is unsuitable;
- (b) that the edaphic factors are unsuitable;
- (c) that avocados cannot compete successfully with trees that do grow in Britain;
- (d) that avocados evolved in some other part of the world and have never reached the British Isles.

Describe, using between ten and twenty short sentences, how you would investigate which of these reasons are justified explanations for the absence of avocado pears.

Section 20.3

Question 8 (Objective 1)

Mark the following statements as either TRUE or FALSE.

- (a) If the numbers in a population are to remain stable, then the pre-reproductive mortality must equal the fecundity.
- (b) For bacteria, which reproduce by each cell dividing into two, a constant rate of reproduction leads to exponential increase in the population.
- (c) Survivorship curves always show a large decrease in numbers early in life.
- (d) If population increase follows a 'logistic curve', the numbers will rise and then remain stable at the maximum value.

Question 9 (Objective 8)

A population consists of 5 adult females and 5 adult males. Assuming that the generations do not overlap and that each female lays 10 eggs and all are fertilized:

How will the population of adults change if the pre-reproductive mortality is: (a) 10%; (b) 50%; (c) 90%?

- (d) What pre-reproductive mortality will give a stable population?

There is no Question 10.

Question 11 (Objective 8)

The following figures apply to sockeye salmon in a Canadian river system. Each female salmon lays 3 200 eggs in a gravelly shallow in the river in autumn.

640 fry (young fish, derived from these eggs) enter a lake near the shallow in the following spring.

64 smolts (older fish, survivors from the fry) leave the lake one year later and migrate to the sea.

2 adult fish (survivors of these smolts) return to the spawning grounds two and a half years later; they spawn and then die.

Calculate the percentage mortalities for sockeye salmon for each of the following periods:

- from the laying of the eggs in autumn to the movement of fry into the lake six months later;
- from entering the lake as fry to leaving the lake as smolts twelve months later;
- from leaving the lake as smolts to returning to the spawning grounds as adult salmon thirty months later.

Draw a survivorship curve for the sockeye salmon in this river system.

What is the pre-reproductive mortality for these sockeye salmon?

Section 20.4

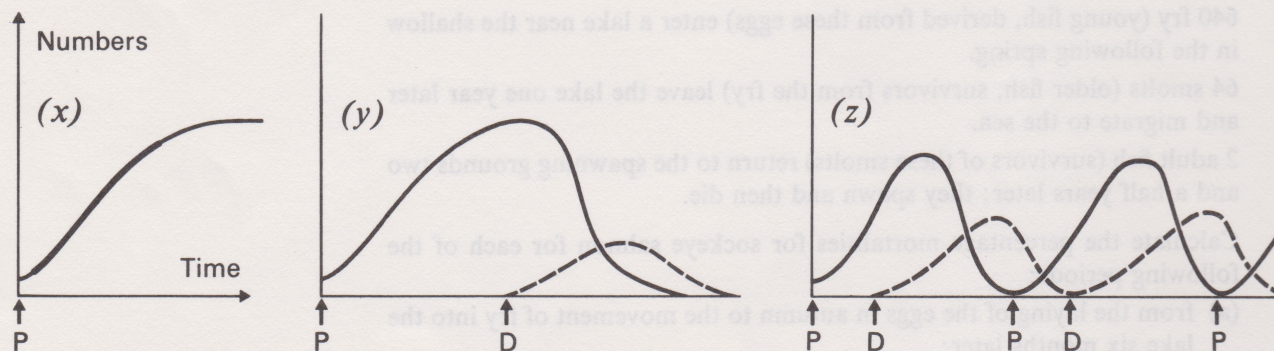
Question 12 (Objective 1)

Mark the following statements as either TRUE or FALSE.

- (a) Herbivores may eat one plant species only.
- (b) Specific parasites each attack many different host species.
- (c) The numbers of herbivores are always limited by their food supply.
- (d) Aggressive behaviour between animals of the same species spaces out individuals or pairs or families over the area.
- (e) Key factors are always density dependent.
- (f) k -values are the same every year.
- (g) Regulating factors are always density dependent.
- (h) Cycles in numbers of predators can often be explained in terms of cycles of prey numbers.

Question 13 (Objectives 6, 7 and 13)

Paramecium and *Didinium* are freshwater ciliate protistans; they are shown on film strip 18(b): numbers 12 and 13. *Paramecium* feeds on bacteria, which are always present in excess in the conditions used for the following experiments; *Didinium* feeds by engulfing *Paramecium*. Look at the three graphs shown, then answer the following questions.



- (a) Graph (x) shows *Paramecium* in a culture medium without any *Didinium*. What is the term used to describe this shape of curve?
- (b) How are the numbers of *Paramecium* increasing along the part of the curve that is shown as a thicker line.
- (c) Graph (y) shows what occurs when a few individuals of *Didinium* are added at the time shown by the arrow to a culture of *Paramecium* similar to that shown in Graph (x). Describe what happens, using not more than three short sentences.
- (d) Graph (z) shows what occurs in a culture to which small numbers of *Paramecium* are added at times indicated by the arrows labelled P and small numbers of *Didinium* are added at times indicated by the arrows labelled D. The numbers of both species then fluctuate in a

cyclical way. Which of the following terms describes the way in which *Didinium* is acting in this experimental system:

- (i) direct density dependent factor;
- (ii) delayed density dependent factor;
- (iii) density independent factor?

If you wish, you could attempt Exercise 4(a) on p. 57 of *Population Dynamics*.

Section 20.5

Question 14 (Objective 10)

If you were in a position to decide whether or not a certain foreign species should be introduced into this country, what types of information would you wish to have available before giving permission for its introduction? Consider this problem with special reference to (a) reindeer; (b) Canadian pondweed; (c) Colorado beetle.

Reindeer live in Scandinavia, feeding on a lichen that also grows on Scottish mountains. Canadian pondweed grows in canals and slow-flowing rivers as well as in ponds and lakes. Colorado beetle lives and feeds on potato plants; it is a native of the USA, but is widely distributed also in Europe.

All sections

Question 15 (Objective 1)

Mark the following statements as either TRUE or FALSE.

- (a) Agriculture is based on mono-culture, which is contrary to the natural development of communities.
- (b) Most weeds are plants that grow slowly and reproduce themselves slowly.
- (c) Pests are usually carnivorous animals.
- (d) Biological control typically involves using organisms that are specific predators or parasites on pests.
- (e) Persistent insecticides are the best possible agents for controlling pest insects.
- (f) There is plenty of protein available now for the human population.
- (g) There will be no problem in producing enough food for twice the present population of the world.
- (h) Problems of energy use and of waste disposal cannot be dissociated from problems of world food supply.

Question 16 (Objective 12)

Some of the following statements about the behaviour of animals relate to this Unit, some to material in Unit 19, and some to general knowledge. Mark each statement as either TRUE or FALSE.

- (a) Camouflage is a defence against predators.
- (b) Camouflage allows predators to attack their prey more effectively.
- (c) Camouflage is a defence against parasites.
- (d) Song is part of courtship behaviour of birds only.
- (e) Song is part of territorial behaviour of birds only.
- (f) Courtship behaviour is one mechanism isolating members of one species from those of closely related species.
- (g) Related species of birds usually look very much alike and have very similar courtship displays.
- (h) Related species of birds nearly always have different courtship displays.
- (i) Many herbivorous animals live in herds or large groups.
- (j) Many carnivorous animals are solitary or live in small groups.

Question 17 (Objectives 9 and 13)

In 1965, the world population of grey seals was estimated as 46 000; of these, 36 000 live round the British Isles. About one-tenth of the British grey seals are based on the Farne Islands (off the coast of Northumberland) for which the following figures are available:

- (a) the number of calves produced annually was about 100 in the 1930s; about 600 in 1952; and more than 1 000 in 1962;
- (b) the seals 'calve' on four islands only—here is information about two of these islands.

	<i>Staple</i>	<i>Brownsman</i>
Number of calves per 100 yds of accessible beach	77	14
Percentage of calves dying during:		
first half of breeding season	16.4	8.7
second half of breeding season	26.4	11.8

Seals are unselective carnivores, their diet includes the following species of fish: salmon, cod, plaice, sand eels, lumpsuckers.

Local fishermen believe that seals prefer lumpsuckers to salmon.

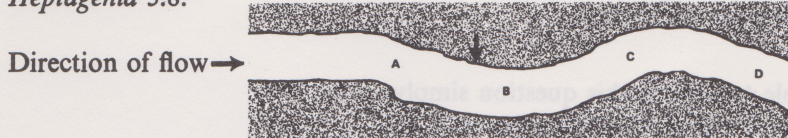
Lumpsuckers eat lobsters.

Use the information given above to construct three arguments *in favour* of action to reduce the number of seals breeding on the Farne Islands and three arguments *against* such action.

Question 18 (Objectives 5, 9 and 13)

The lowest levels of dissolved oxygen as cm^3 per litre which can be tolerated by the following organisms are:

Tubifex 0.2; *Erpobdella* 2.0; *Chironomus riparius* 0.5; *Limnaea pereger* 1.7; *Asellus* 1.8; *Baetis rhodani* 3.0; *Gammarus* 3.2; *Ancylus* 2.8; *Phoxinus* 6.0; *Heptagenia* 5.8.



In the river above, the fauna at sites A, B, C and D were as follows:

A	B	C	D
<i>Phoxinus</i> , <i>Heptagenia</i> , <i>Gammarus</i> , <i>Ancylus</i> , <i>Baetis</i> , <i>Limnaea</i>	<i>Tubifex</i> only	<i>Chironomus</i> only	<i>Chironomus</i> , <i>Erpobdella</i> , <i>Asellus</i> , <i>Limnaea</i>

Suggest what happened to the river at the point marked by the arrow.
What does the change in fauna between B and D indicate?

Question 19 (Objectives 9 and 13)

Charles Darwin quoted the following figures:

100 heads of red clover produced 2 700 seeds, but the same number of heads protected from the attention of humble-bees produced not a single seed. He quoted Colonel Newman as saying 'more than two-thirds of them (i.e. humble-bees) are destroyed all over England' by field-mice, and also 'near villages and small towns I have found the nests of humble-bees more numerous than elsewhere'.

Darwin put forward the following hypothesis:

'... the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district'.

Read the following statements, then arrange some of them in a sequence to support Darwin's hypothesis.

Try to arrange some of the statements in a sequence to form a different hypothesis.

- Elderly ladies who keep cats choose to live in villages rather than in solitary cottages.
- Farmers often have granaries infested with rats and mice.
- Cats kill field-mice.
- Farmers cut down trees except sometimes along field boundaries.
- Humble-bees nest in burrows in short grass.
- Owls feed on small rodents including field-mice.
- Many houses in villages have gardens with lawns and trees.
- Owls wait in trees and pounce when they hear a rustle of small animals in the grass.
- Farmers keep cats to control rats and mice in their buildings.

Question 1

- (a) False, see 20.0.
- (b) True, see 20.1.
- (c) True, see 20.1.
- (d) False, see 20.1.
- (e) False, see 20.1.1 and *Ecological Energetics* 1.6 and 2.4.
- (f) True, see 20.1.2.
- (g) You should have found it impossible to answer this question simply as true or false. The *biomass* of carnivores is generally less than that of herbivores (see *Ecological Energetics* 2.4); but in some communities the herbivore biomass is small and the carnivores eat detritus feeders (decomposers) as described in *Ecological Energetics* 3.2 and 3.3. The number of carnivores is generally smaller than the number of herbivores, but this is not true where the bulk of carnivore food is provided by decomposers.
- (h) True, see *Ecological Energetics* 2.4.

Question 2

The roach food intake must supply the energy for respiration and production: $460 + 118 = 578 \times 10^3 \text{ J m}^{-2}$ per annum.

This roach food includes bottom fauna and plant material. The amount of plant material must be: total food – bottom fauna = $578 - 114 = 464 \times 10^3 \text{ J m}^{-2}$ per annum.

Bleak food includes bottom fauna and surface drift. The amount of surface drift must be: total food – bottom fauna = $670 - 310 = 360 \times 10^3 \text{ J m}^{-2}$ per annum. This bleak food intake supplies energy for production and respiration so the amount of energy dissipated in respiration is: total food – production = $670 - 147 = 523 \times 10^3 \text{ J m}^{-2}$ per annum.

If you feel uncertain about the basis for these calculations, read *Ecological Energetics* 3.2 and the commentary on it in the text under 20.1.1.

Question 3

This is an exercise based on understanding ecological pyramids and energy flow diagrams (see *Ecological Energetics* 2.4 and 3.2 and the commentary in this text under 20.1.1).

- (a) P (herbivores) = winter moth caterpillars; Q (first carnivores) = predatory beetles; R (second carnivores) = shrews; S (top carnivore) = owl.
- (b) z (plants) = oak-trees; y (herbivores) = winter moth caterpillars; x (first carnivores) = predatory beetles; w (second carnivores) = shrews. If w is taken to include all carnivores above the first level, then owls are also included.
- (c) A (herbivores) = winter moth caterpillars.

Arrow 5 represents their respiration: $30 \times 10^4 \text{ J m}^{-2}$.

Arrow 1 represents their consumption of energy, which equals their production + their respiration: $35 \times 10^3 + 30 \times 10^4 = 33.5 \times 10^4 \text{ J m}^{-2}$.

B (first carnivores)=predatory beetles.

Arrow 6 represents their respiration: $12.5 \times 10^4 \text{ J m}^{-2}$.

Arrow 2 represents their consumption of energy, which equals their production + their respiration:

$$12.5 \times 10^4 + 12.5 \times 10^3 = 13.75 \times 10^4 \text{ J m}^{-2}.$$

C (second carnivores)=shrews.

Arrow 7 represents their respiration: $12.5 \times 10^3 \text{ J m}^{-2}$.

Arrow 3 represents their consumption of energy, which equals their production + their respiration: $125 + 12.5 \times 10^3 = 12.63 \times 10^3 \text{ J m}^{-2}$.

D (top carnivores)=owls.

Arrow 8 represents their respiration: $21 \times 10^2 \text{ J m}^{-2}$.

Arrow 4 represents their consumption of energy, which equals their production + their respiration: $12.5 + 21 \times 10^2 = 21.13 \times 10^2 \text{ J m}^{-2}$.

Compare the production of each organism in the food chain with the consumption of the organism which feeds on it—if an organism is the sole source of food for the next consumer, then the production of the food organism will be at least one order of magnitude greater than the consumption of the organism that eats it. If this is not so, the population of the food organism will probably decrease in biomass and become extinct.

Oak-tree production is 50×10^5 , winter moth caterpillar consumption is 33.5×10^4 , so these caterpillars could feed entirely on oak-trees.

Winter moth caterpillar production is 35×10^3 ; beetle consumption is 13.8×10^4 so the winter moth population could not support the beetles. The predatory beetles must have other sources of food energy—in fact, they eat a variety of species of insects.

Beetle production is 12.5×10^3 ; shrew consumption is 12.6×10^3 ; so the shrews must have other sources of food in addition to predatory beetles.

Shrew production is only 125, but owl consumption is 21×10^2 ; so the owls must have sources of food in addition to shrews. (In fact, owls usually do not eat shrews; they prey on other small mammals such as field-mice, voles and moles—see Appendix 1.)

Question 4

If you cannot answer this question, you should read 20.1 and 20.1.2 again.

From the metabolic point of view, the organisms fall into three groups:

- photosynthetic autotrophes: oak-tree and grass. Statements 3, 5, 6, 7, 8 and 9 are true for these.
- heterotrophes that consume living or freshly killed organisms: caterpillars (herbivores), owl (carnivore) and man (omnivore). Statements 2, 6 and 7 are true of these. You may have put man in a special category, since some of these conversions can be carried out in laboratories or factories as a result of human activity (e.g. 4) but this is not part of 'human metabolism'.
- heterotrophes that are decomposers: decomposing bacteria. Statements 1, 2, 6 and 7 are true of these. Statement 4 is true of a different group of bacteria, the 'nitrogen-fixing bacteria'.

Question 5

- (a) False, see 20.2.
- (b) True, see 20.2.1.
- (c) False, see 20.2.
- (d) False, see 20.2.1.
- (e) True, see 20.2.2.
- (f) False, see 20.2.2.

Question 6

- (a) The temperature in Lake Victoria is usually close to 25° C. This is well within the tolerance of cyprinid and cichlid fishes (and both groups are present there), but it is dangerously close to the upper limit for salmonid fishes (which are not native there).
- (b) Great Bear Lake freezes in the winter and remains cool through the summer. Cichlid fishes could not live there, but salmonid and cyprinid fishes could.
- (c) Lake Balaton freezes in the winter and becomes very warm in the summer. Cichlid fishes could not survive the winter and salmonids could not survive hot summers; it should support (as it does) cyprinid fishes.
- (d) Fish ponds in Malaya and Nigeria contain warm water all through the year. This is ideal for cichlid and cyprinid fishes, but salmonids could not survive.
- (e) The water temperature may fall to freezing in the winter in Sweden and Ireland, but it remains cool in the summer. These ponds are ideal for salmonid fishes (such as trout) and cyprinids can also live in them; cichlids would not survive through most of the year.
- (f) In Israel and Poland, the water becomes very cold and may freeze in winter; it becomes very warm in summer. Cichlids would not survive through the winter nor salmonids through the summer; these are ponds for rearing cyprinid fishes (such as carp).

Question 7

To investigate whether the climate (a) and edaphic factors (b) in Britain are suitable for avocado trees or not, you could try to cultivate avocado nuts in different parts of Britain. You would use local soils under greenhouse conditions (with temperature and light adjusted appropriately—see under (d)) to investigate edaphic factors. You would grow the plants out-of-doors but in prepared compost or humus to investigate climate. You would grow the plants out-of-doors and in the local soil to investigate any interaction between soil and climate.

You would not be able to investigate (c) unless the plants could survive both the British climate and in at least one type of British soil. If they could survive, then you could plant them out with seedlings of trees and compare survival under these conditions with survival under non-competitive conditions.

To investigate (d) you would find out from books and scientific papers where avocados grow wild and whether there is information to show that they are native to those areas or have been introduced. Eventually you might be able to locate a limited part of the world that represents their natural distribution. You would know as a result of your researches the type of climate in which avocados grow or can be cultivated and you could use this information in your greenhouse experiments.

Read 20.2.2 if you need to remind yourself about the factors affecting the distribution of plants.

Question 8

- (a) False, see 20.3. Births minus deaths must equal parent numbers.
- (b) True, for the early growth of bacteria in a culture medium; the growth of the population later declines giving a 'logistic' curve, see 20.3.1.
- (c) False, since some curves, such as that for man, do not follow this pattern; other curves do show this early decrease in numbers, see 20.3.
- (d) True, see 20.3.1.

Question 9

The 5 females will lay 50 fertilized eggs.

- (a) if the pre-reproductive mortality is 10 per cent, the offspring generation will be 45
- (b) if the pre-reproductive mortality is 50 per cent, the offspring generation will be 25
- (c) if the pre-reproductive mortality is 90 per cent, the offspring generation will be 5.

So for (a), the offspring population will be 4.5 times the parent population.

So for (b), the offspring population will be 2.5 times the parent population.

So for (c), the offspring population will be 0.5 times the parent population.

- (d) For a stable population of 10 adults in each generation, 10 offspring must survive from the 50 eggs. Since 40 offspring must die, the mortality must be 80 per cent.

There is no Question 10.

Question 11

- (a) Out of 3 200 eggs, 640 survive, so 2 560 die—a mortality of 80%.
- (b) Out of 640 fry, 64 survive, so 576 die—a mortality of 90%.
- (c) Out of 64 smolts, 2 survive, so 62 die—mortality of about 97%.

The total pre-reproductive mortality for salmon is 3 198 out of 3 200—99.97%.

3 200 eggs→640 fry→64 smolts→2 adult salmon.



Question 12

- (a) True, see 20.2 and 20.4.3.
- (b) False, the meaning of 'specific' is that this type of parasite is limited to one host species or a small number of related species, see 20.4.2.
- (c) False, see 20.4.3.
- (d) True, see 20.4.
- (e) False, usually they are independent of density, see 20.4.1.
- (f) False, see 20.4.1.
- (g) True, if delayed density dependent factors are included, see 20.4.2.
- (h) True, see 20.4.4.

Question 13

- (a) This is a 'logistic' curve—compare it with Figure 3.3 of *Population Dynamics*.
- (b) Exponentially, see 20.3.1.
- (c) *Didinium* consumes *Paramecium* faster than the latter can reproduce themselves. *Didinium* increases in numbers until it is limited by its decreasing food supply; then the numbers begin to fall. Both *Paramecium* and *Didinium* become extinct.
- (d) It is acting as (ii) a delayed density dependent factor. The peaks and troughs of *Didinium* numbers follow the peaks and troughs of *Paramecium* numbers regularly.

Question 14

You would wish to know the possible effects of introducing the foreign species into British communities of plants and animals. The foreign species could affect native species (cultivated and wild) through food web relations (by consumption or competing for a food supply or altering the food web in other ways) or through the introduction with it of pests or diseases that might have a devastating effect on native organisms. The latter problem could be mitigated by quarantining the organism—cultivating it under isolation so as to clear it of pests and diseases as far as possible. The problem of effects through food web relations could be clarified by considering the species' food web relations in its native environment. To take our three examples.

- (a) Reindeer are herbivores with a limited food preference—they would not compete with native sheep or cattle or native deer. Their activity might lead to soil erosion through eating out of lichens—the probability of this could be judged by comparing the environment in Scandinavia with that in Scotland. It is unlikely that native predators would be able to tackle such large animals. Reindeer are now herded near Aviemore in Scotland.
- (b) Canadian pondweed was introduced into Britain in 1842; it propagated itself so vigorously that it soon choked drainage ditches in the Fens and also some rivers and canals. After flourishing at a nuisance level between 1850 and 1880, it began to propagate less luxuriantly (the cause for this is not understood). Now it is a very common plant and

is considered useful since it adds much oxygen to the water and supports many animals that are valuable foods for fishes. An experimental introduction in conditions where the plant could not spread to other waters might have revealed its undesirable (in the short term) vigour but not its long-term usefulness.

- (c) The colourful Colorado beetle is a pest in the USA and in Europe. A very brief investigation of the devastation it causes to potato fields in both continents would be sufficient to convince any reasonable person that it should be kept out of the British Isles. In fact, there are regulations forbidding its introduction here. Small numbers of live beetles have occasionally been found in southern counties in summer; immediate efforts to eradicate them before the species could become established have so far been successful.

Question 15

- (a) True, see 20.6.
- (b) False, see 20.6.
- (c) False, most pests are probably herbivores, see 20.6.1.
- (d) True, see 20.6.1.
- (e) False, see 20.6.1.
- (f) False, see 20.6.2.
- (g) False, there are already problems with the present population, see 20.6.2.
- (h) True, see 20.6.2.

Question 16

- (a) True—provided that the predators hunt mainly by sight; remember the peppered moth shown in TV 19.
- (b) True—provided that the prey detect predators by sight; think of lions concealed on dry grassland and tigers in forests.
- (c) True—only if parasites find their hosts by sight; this is unusual—most parasites are probably attracted by scents.
- (d) False—it is part of courtship but also usually part of other aspects of behaviour.
- (e) False—it is part of territorial behaviour but also usually part of courtship behaviour also.
- (f) True—see 19.7.2.
- (g) False—they may resemble each other but their courtship behaviour is usually markedly different—see 19.7.2. (Consider ducks in parks).
- (h) True—this is the converse of (g).
- (i) True—think of antelopes, zebra, caribou and buffaloes.
- (j) True—think of lions and eagles.

Question 17

Possible arguments in favour of reducing the number of seals that breed on the Farne Islands are as follows.

- 1 Seals eat salmon, cod and plaice, all valuable fishes (they also damage salmon nets by taking fish out of them)—and thus reduce our potential food supply.
- 2 The number of seals has increased so markedly since the 1930s that it appears that any natural balance has been upset and the numbers may just go on increasing indefinitely.
- 3 Where there are many seals, there is a higher mortality of calves; to allow the total number of seals to go on increasing will lead to greater suffering among calves; to reduce the number of seals will reduce suffering.

Possible arguments against reducing the number of seals that breed on the Farne Islands are as follows.

- (a) The grey seal is a rare species; 75 per cent of the world population lives in British waters; we have a responsibility to protect them so it would be wrong to kill any.
- (b) Reducing the number of seals will mean more lumpsuckers and hence fewer lobsters; lobsters are a prized delicacy which should be protected.
- (c) Since the proportion of calves dying is higher where the seals are more crowded, reducing the number of breeding seals may not in fact reduce the number of adults because the total number of calves surviving may be the same as at present. This death of calves may be the regulating factor—interference with this may lead to unexpected results.

Question 18

The fauna at point A includes animals which require high levels of dissolved oxygen (e.g. *Phoxinus* 6.0, *Heptagenia* 6.8), so here there must be at least 7 cm³ of dissolved oxygen per litre.

At B, only *Tubifex* is present, suggesting that the level of dissolved oxygen must be between 0.2 and 0.5 cm³ per litre. Therefore something happened to the river at the point marked by the arrow resulting in a fall in dissolved oxygen. At D, the level must be at least 2.0 cm³ per litre (since *Erpobdella* lives there). Therefore as it flows from B to D, the amount of dissolved oxygen in the water increases from 0.5 to 2 cm³ per litre.

These are the kind of changes in dissolved oxygen and in river fauna that occur when poorly treated domestic sewage enters a river (at the point marked by the arrow) and causes pollution from which the river gradually recovers as it flows on.

Question 19

Darwin assumes that the number of field-mice determines the number of bees and that clover plants will grow only where bees have visited the flowers. If there are more bees near villages and small towns, this implies that there are fewer field-mice there. Darwin suggests that the low numbers of field-mice are the result of the presence of many cats near villages and small towns.

Of the nine statements, (e) followed by (g) account for the presence of humble-bees near villages; (c) followed by (a) account for the absence of field-mice near villages; (i) implies that there could be many cats in the countryside but (b) explains that these cats probably hunt in granaries and do not molest the field-mice that eat the humble-bees. So Darwin's hypothesis is supported by the observations in statements (e), (g), (c), (a), (i) and (b).

An alternative hypothesis is supported by statements (e), (g), (f), (h), (d) and (g) again. It is that the number of field-mice is controlled by owls; these birds hunt from trees; there are few suitable trees in the countryside because farmers cut them down, but there are suitable trees in village gardens; hence there are fewer field-mice near villages and therefore (from Colonel Newman's statement) more humble-bees and so probably more clover (from Darwin's own statement).

Legends for Filmstrips

Filmstrip 19/20a

- 1 Eggs ($\times 60$) and larva ($\times 20$) of the fruitfly *Drosophila melanogaster*. One egg is shown seen from the side (with two hornlike spiracles (breathing tubes) sticking up); the other egg is seen from above with the two spiracles flattened outwards. The larva is a small maggot.
- 2 Two puparia of *Drosophila melanogaster* ($\times 20$). The adult insect is developing inside the hard case of the puparium.
- 3 Anaesthetized adult fruitflies, *Drosophila melanogaster* ($\times 10$). Note the general resemblance to small houseflies and the characteristic colour pattern. Compare these flies with the drawings in your Home Experiment notes for Unit 20.
- 4 Adults of two common species of fruitfly ($\times 10$). On top is *Drosophila melanogaster* (compare with photograph 3) and below is *Drosophila subobscura*. Note the differences in size and colour pattern between these two species. Compare the photograph with the drawings in your Home Experiment notes for Unit 20.
- 5 Two parasites of the fruitfly *Drosophila*. These were both bred from wild *Drosophila* populations reared as described in your Home Experiment notes for Unit 20. Compare these two specimens with the photographs of the adult fruitflies (3 and 4): note the differences in body shape (the parasites are both wasps with slender waists), in wing shape and pattern and in length of antennae (feelers). A live specimen of *Phaenocarpa* (5b) is shown in the TV programme for Unit 20; the other parasite (5a) is called *Pseudeucoila*. If you collect either of these two insects while carrying out your Home Experiment for Unit 20, preserve the specimen and inform us.
- 6 Mouse chromosomes (Unit 19) ($\times 1\,000$) shortly before the first meiotic division. Note that each is divided into two chromatids. Attempt to count the number of chromosomes.
- 7 Mouse chromosomes ($\times 1\,000$). The chromosomes have become associated in homologous pairs, each pair comprising four chromatids. Count the number of pairs.
- 8 A further enlargement of one homologous pair of chromosomes, clearly showing chiasma formation and the physical crossing-over of the chromatids.

Filmstrip 20b Photographs of British vegetation

- 1 Oakwood on clay soil, photographed in spring. Note the herbs under the trees, which are not yet in full leaf. (Forestry Commission.)
- 2 Oakwood on clay soil. Bluebells are in flower under some hazel shrubs. (G. E. Simmons.)
- 3 Oakwood on dry sandy soil. Note the dense undergrowth of bracken. (E. V. Rogers.)
- 4 Norway Spruce. Note the close spacing of trees and absence of undergrowth. (Forestry Commission.)
- 5 Lullington Heath, Sussex: photograph taken on 23 March 1954. Note the rabbit burrows surrounded by bare chalk, the short turf and the elder bushes. Rabbits were common here. (Nature Conservancy.)
- 6 Lullington Heath, Sussex: photograph taken on 21 February 1967. This is the same area that as shown in (5). Note the dense sward of grass and the tangle of bramble bushes in front of the elder bush. Rabbits had died of myxomatosis. (Nature Conservancy.)
- 7 Old Winchester Hill, Hampshire: photograph taken on 10 August 1954. Note the presence of chalk lumps forming scree and the large numbers of ragwort plants (with yellow flowers). Rabbits were common here. (Nature Conservancy.)

- 8 Old Winchester Hill, Hampshire: photograph taken on 13 August 1956. This is the same view as that in (7). Note that the turf has grown over most of the scree; there are no ragwort plants. Rabbits had died of myxomatosis.

Filmstrip 20c Moths, caterpillars and their parasites

- 1 A 'wingless' female winter moth on the trunk of an oak-tree. Note the short wings, long legs and abdomen swollen with eggs.
- 2 Winter moth, *Operophtera brumata*: wingless female and winged male mating – photographed by flash at night in November on the trunk of an oak-tree.
- 3 Winter moth caterpillar photographed in May on an oak twig.
- 4 *Cyzenis*, a fly whose larva is a parasite of the winter moth caterpillar. On the left, a dead 'Museum' specimen, on the right, a live fly. Note the similarity to houseflies.
- 5 *Cratichneumon*, a wasp whose larva is a parasite of the winter moth pupa. Male (left) and female (right), each mounted above the winter moth pupal case (chrysalis) from which it emerged.
- 6 November Moth, *Oporinia dilutata* caterpillar on an oak twig with the young leaves beginning to unfold in April. The adult moth is about in October and November.
- 7 Scarce Umber caterpillar photographed in May on an oak leaf.
- 8 Scarce Umber, *Erannis aurantiara*: wingless female and winged male on the trunk of an oak-tree in November. Note the similarity to the winter moth (2).

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Notes

S.100—SCIENCE FOUNDATION COURSE UNITS

- 1 Science: Its Origins, Scales and Limitations
- 2 Observation and Measurement
- 3 Mass, Length and Time
- 4 Forces, Fields and Energy
- 5 The States of Matter
- 6 Atoms, Elements and Isotopes: Atomic Structure
- 7 The Electronic Structure of Atoms
- 8 The Periodic Table and Chemical Bonding
- 9 Ions in Solution
- 10 Covalent Compounds
- 11 } Chemical Reactions
- 12 }
- 13 Giant Molecules
- 14 The Chemistry and Structure of the Cell
- 15 } Cell Dynamics and the Control of Cellular Activity
- 16 }
- 17 The Genetic Code: Growth and Replication
- 18 Cells and Organisms
- 19 Evolution by Natural Selection
- 20 Species and Populations
- 21 Unity and Diversity
- 22 The Earth: Its Shape, Internal Structure and Composition
- 23 The Earth's Magnetic Field
- 24 Major Features of the Earth's Surface
- 25 Continental Movement, Sea-floor Spreading and Plate Tectonics
- 26 } Earth History
- 27 }
- 28 The Wave Nature of Light
- 29 Quantum Theory
- 30 Quantum Physics and the Atom
- 31 The Nucleus of the Atom
- 32 Elementary Particles
- 33 } Science and Society
- 34 }